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Zooplankton Grazing and Population Dynamics Relative to Water Quality in Southern Lake Huron

State Univ. of New York at Albany

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ZOOPLANKTON GRAZING AND POPULATION DYNAMICS RELATIVE TO WATER QUALITY IN SOUTHERN LAKE HURON

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FOREWORD

Our nation's freshwaters are vital for all animals and plants, yet our diverse uses of water--for recreation, food, energy, transportation, and industry--physically and chemically alter lakes, rivers, and streams. Such alterations threaten terrestrial organisms, as well as those living in water. The Environmental Research Laboratory in Duluth, Minnesota develops methods, conducts laboratory and field studies, and extrapolates research findings

--to determine how physical and chemical pollution affects aquatic life

--to assess the effects of ecosystem on pollutants

--to predict effects of pollutants on large lakes through use of models

--to measure bioaccumulation of pollutants in aquatic organisms that are consumed by other animals, including man

This report, as part of the Large Lakes Research Program, examines the relationship of zooplankton to water quality in one of the Great Lakes. The knowledge of the relationship between zooplankton and phytoplankton is essential when attempting to understand a Great Lakes ecosystem. This report details the relationship between water quality and zooplankton populations in Lake Huron. The effects of various phytoplankton forms of zooplankton grazing is also discussed in relation to water quality.

Norbert Jaworski, Ph.D.
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Duluth, Minnesota

ABSTRACT

Planktonic herbivores controlled the growth of phytoplankton in the open waters of Southern Lake Huron during the late summer and fall; larger algae remained untouched during the spring diatom bloom. Over a growing season these crustaceans grazed 0.3 to 41.9% of the standing crop of phytoplankton. Immature copepods (nauplii and copepodites) were the most effective grazers. Selective grazing by crustaceans centered on nannoplankton (< 22 µm diameter), whereby 92 to 2840% of the daily productivity was grazed by large cladocerans and immature copepods. In contrast, netplankton was harvested to a much lesser degree. Laboratory experiments reinforced this picture of selective cropping. Presently in Lake Huron such selective grazing accounts for an effective biological control over algal production; such control will be lost if these phytoplankton populations are allowed to shift to ones dominated by large blue-green algae. Populations of herbivores were also used to characterize water quality. Generally outer Saginaw Bay and most inshore waters were of lower water quality than offshore surface waters. These inshore areas also had the highest productivity of zooplankton.

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SECTION 1

INTRODUCTION

PURPOSES

The objectives of this investigation involved a) determining the magnitude of grazing on natural phytoplankton populations in Southern Lake Huron, b) collecting experimental field evidence for selective grazing on specific size-groups of phytoplankton, c) providing experimental laboratory evidence concerning the mechanisms of selective herbivory, d) formulating a measure of biological control by herbivorous crustaceans, and e) determining the abundance of the crustacean zooplankton in Southern Lake Huron, both by net sampling and modern acoustical techniques.

ROLE OF GRAZERS

Detailed estimates of grazing by the herbivorous zooplankton are necessary to understand the degree to which biological control of algal populations occurs. Likewise, since the control of a size-class or taxonomic grouping of algae may mean the stimulation or release from competition of another group of primary producers, numerous interactions may exist between the grazers, their predators, and their algal prey. Each of these must be understood in itself before we may truly understand the functioning of aquatic systems.

The impact of the grazers upon a natural assemblage of phytoplankton is controlled by a series of interactions affecting grazing both quantitatively and qualitatively. These include the interaction between the ingestion rate of the zooplankton and the abundance of algae; ingestion by zooplankton often saturates at 10^5 cells ml^{-1} for freshwater organisms (McMahon and Rigler, 1963); the relationship between grazing selectivity by zooplankton and the relative abundance of preferred algal foods (Bogdan and McNaught, 1975); the differential resistance to digestion of algal foods (Porter, 1973); temperature of the environment and Q_{10} for ingestion; and assimilation of a particular species and daily and seasonal fluctuations in grazing behavior, related either to apparent endogenous rhythms in grazing (Chisholm, Stross, and Nobbs, 1975) or to the inhibition of grazing by substances released into the environment.

In designing a study of an aquatic ecosystem, attention should be focused on three basic processes, including seasonal and daily patterns of grazing by zooplankton, remineralization of algal nutrients by zooplankton, and selective cropping of large zooplankters by fish predators. These factors imply that a considerable amount of self-regulation occurs in aquatic ecosystems. As algal production increases with the input of nutrients from an urbanized society, not only does zooplankton grazing increase, but the remineralization or recycling of important nutrients changes correspondingly.

The purpose of this report is to examine the first of these three important interactions: the seasonal and diel (daily) patterns of grazing by the crustacean zooplankton of Lake Huron. Due to technical difficulties, we did not attempt to directly measure the component assigned to the rotifers, nor did we estimate grazing on bacteria and detritus, since this component is of lesser importance, even in eutrophic ponds (Saunders, 1969), and bacteria are probably not the major food source for the herbivorous zooplankton in mesotrophic Lake Huron.

SECTION 2

CONCLUSIONS

Planktonic herbivores have many functions in Southern Lake Huron, a natural unperturbed aquatic system. They feed upon both algae and detritus. In doing so they may remove very little of the standing crop of phytoplankton at the upper extreme of sizes, whereas at the lower extreme they may selectively remove entire groups of algal species. Thus, the impact of grazing rarely affects the entire assemblage, but may result in the inhibition or stimulation of specific algal groups. Grazers not only selectively influence the phytoplankton through consumption, but also remineralize important amounts of algal nutrients, thereby stimulating ungrazed algae. Ultimately successful groups of herbivores provide important food resources for larval fishes. Thus, herbivore dynamics must be understood to model and manage aquatic ecosystems like Southern Lake Huron. In this study we have determined the level of both total and size-selective grazing by crustaceans in Southern Lake Huron.

Crustaceans graze from 0.1 to 37.8% of the net primary productivity and 0.3 to 41.9%d^{-1} of the standing crop of phytoplankton in Southern Lake Huron. Grazing is generally high in early summer and fall and low during both the spring diatom bloom and the mid-summer blue-green bloom. The immature stages of copepods were the most effective grazers, including populations of nauplii, calanoid copepodites, and cyclopoid copepodites. At the organismal level, mass ingestion rates (% body weight ingested day^{-1}) were highest for nauplii (100%), cyclopoid copepodites (100%), *Cyclops bicuspidatus* (103%), and *Diaptomus* adults (100%) and lowest for *Limnocalanus* (0.5%). Thus, it was not surprising that the percentage assimilation of ingested food was highest for rapidly growing nauplii and copepodites abundant in this ecosystem and lowest for a predaceous calanoid copepod. Grazing rates appeared to be closely related to temperature and the presence of large diatoms and blue-green algae. Grazing was not limited by populations of algae exceeding the saturation level for crustacean grazing, since Southern Lake Huron is oligotrophic and its waters were characterized by phytoplankton populations well below 10^5 cells ml^{-1}.

The nannoplankton (algae < 22 μm diameter) were selectively grazed by zooplankton. From 92% to 2839% of the net primary productivity of nannoplankton was removed each day of the 6 months constituting the growing season. This exceptional harvest was due to selective grazing by the cladocerans Holopedium gibberum, Eubosmina coregoni, and Daphnia retrocurva, and copepod nauplii, cyclopoid copepodites, and calanoid copepodites. Relatively little harvest of nannoplankton was attributable to adult Diaptomus. In contrast, only 30% to 367% of the netplankton net primary productivity was ingested. The harvest of netplankton, in contrast, was due in part to the same cladocerans (Holopedium, Eubosmina), but with much less netplankton ingestion accomplished by copepods. During August, the cladocerans grazed 297% of netplankton production, as opposed to 26% by calanoids and 44% by cyclopoids. Considering the size of these herbivores, Chydorus sphaericus (21.9%d^{-1}) and nauplii (21.2%d^{-1}) exhibited the highest mass ingestion rates (% body weight d^{-1}) and Diaptomus spp. (adults), the lowest (2.4%d^{-1}) on nannoplankton. On netplankton, Chydorus sphaericus (12.7%d^{-1}) had the highest mass ingestion rate. Generally those animals which ingested large amounts also egested large amounts, such that assimilation was inversely related to ingestion. Diaptomus minutus and Cyclops bicuspidatus adults assimilated most of the small volume of netplankton they ingested, whereas Holopedium and calanoid copepodites, while efficient ingestors, were inefficient assimilators of nannoplankton. Generally, assimilation rates on nannoplankton (mean 54.3 ± 13.4%; range 5-100%) were much higher than on netplankton (mean 29.3 ± 8.0%; range 3.4-83.3%), due in part to the protective gelatinous sheath surrounding many blue-green algae.

Grazing exerted a significant biological control upon the growth of algal populations in Southern Lake Huron. Biological control exists when the daily production of a resource is totally grazed. Control through the natural populations of crustacean herbivores existed from early May through late October 1975, with up to 25.3x the daily production of nannoplankton harvested during August. In contrast, biological control over netplankton growth existed over the same period, but with a maximum of 367% harvested. We emphasize that the primary productivity of oligotrophic waters of Lake Huron is in balance with the grazers, due to the apparently rare inhibition of grazing by blue-green algae. Algal growth must be kept under control.

Laboratory experiments permitted enumeration of those algal characteristics which limited grazing. Both Diaptomus sicilis and cyclopoid copepodites were highly selective grazers. They both selected large plain cells, consumed small plain cells in the proportion offered, and rejected small and large sheathed cells, as well as small spined cells. It is not surprising that blooms of nuisance algae are characterized by blue-greens which have sheaths. Size-selective grazing was further investigated in the field using micro-beads made of polystyrene, added to natural algal foods. Diaptomus (nauplii, copepodites, and adults) and Cyclops bicuspidatus (adults) both selected very small beads, less than 1 μm in diameter, illustrating again the intense selective pressures which occur upon those small phytoplankton characteristic of oligotrophic lakes, such as Lake Huron.

Eutrophic waters are characterized by communities of crustaceans peculiar to warm waters and most likely associated assemblages of algae and groups of predatory fishes. Cyclopoid copepods and cladocerans are often considered eutrophic indicators and were found in abundance in inshore waters of Lake Huron and particularly in the mouth of Saginaw Bay. Calanoid copepods are more oligotrophic organisms. All were found offshore, but the most oligotrophic, Diaptomus sicilis, was most abundant in the midlake region.

Planktonic ratios (calanoids/cyclopoids and cladocerans) and indicator species were utilized to structure water quality within the eight management segments of Southern Lake Huron. The inshore segments (4, 5, 7, 8) and segment 6 offshore of Saginaw Bay consistently showed lower water quality than segment 10 (northern open waters). Significant increases in pollution-indicating crustaceans were not apparent between samples collected by Canadian Center for Inland Waters (CCIW) in 1971 and ourselves in 1974; historical trends must be examined over longer intervals to be evident.

The horizontal distribution of total crustacean biomass was examined, both by net sampling and through acoustical integration of echoes from these small targets. Net sampling showed that zooplankton biomass was greatest in the mouth of Saginaw Bay. Frequently, large densities moved counter clockwise from the bay and drifted southward along the Michigan shoreline. Inshore densities were also of importance, with notable areas of high standing crops near Goderich, Canada. Acoustic estimates of particle abundance likewise showed maxima in the mouth of Saginaw Bay. However, in contrast to net sampling, deepwater maxima of biomass were also observed through the use of acoustic estimates. This discovery is explained by the suggestion that these large deepwater particle densities are aggregations of detritus.

SECTION 3

RECOMMENDATIONS

The waters of Southern Lake Huron are of high water quality, as evidenced by populations of oligotrophic, cold water calanoid copepods. Dominant herbivores today maintain a desirable balance between grazing (removal) and production of phytoplankton. That is, a natural biological control exists upon phytoplankton growth (both nannoplankton and netplankton). Zooplankton selectively graze small phytoplankters. Most species of zooplankton, however, ignore certain large sheathed blue-green algae. Such colonial blue-greens occur in nutrient enriched environments; their growth also may show lesser acute effects from chlorinated hydrocarbons. Since intense biological control of nannoplankton is a natural ecosystem characteristic, any combination of nannoplankton inhibition (by grazing) and netplankton stimulation (by nutrient enrichment and selective poisoning of nannoplankton) will lead to a shift in dominance by blue-green algae and troublesome blooms.

Currently the high water quality of Southern Lake Huron, reflected in the presence of dominant populations of calanoids, can be maintained by shrewd ecosystems management. We recommend the usual reduction of inorganic limiting nutrients (P), coupled with a reduction in toxicant loadings. Also, the management of planktonphagous fishes (chiefly the alewife) is necessary to maintain the endemic herbivore population. If these four objectives are met, biological control by crustaceans upon algal populations should continue in Southern Lake Huron.

Warnings of potential changes are evident. The largest standing crops of zooplankton, dominated by the eutrophic *Bosmina longirostris*, were found in the mouth of Saginaw Bay. *Bosmina* was shown to be an ineffective grazer, even when abundant. In addition, other eutrophic forms including the calanoid *Diaptomus siciloides* were found in the bay. Thus, zooplankton populations in the bay were typical of eutrophic waters. We suspect that such herbivore populations do not control algal production in the bay (a matter of current investigation). While the waters of the main lake may never resemble those of the shallow bay, the trend, unless reversed, will be toward reduced water quality.

SECTION 4

EXPERIMENTAL PROCEDURES

4.1 METHODS FOR TOTAL GRAZING

A modification of the original methods of Nauwerck (1959), who determined grazing through the use of tagged (^{14}C) phytoplankton, was employed. The radioactivity of zooplankton was measured after a brief feeding period (15 to 30 min) too short for the production of radioactive faeces at low food levels. Basic to this method is the estimation of the shortest time in which a particle of food can pass the gut, or in which significant amounts of $^{14}CO_2$ can be respired. Previous investigators have estimated this period to be 10 to 20 min (Bogdan and McNaught, 1975). Before being given radioactive food, the animals were acclimated for 1 hr in non-radioactive cells of the same natural assemblage tagged with $Na^{14}CO_3$. Approximately 2000 animals were acclimated in 600 ml of natural algae in lakewater. After 1 hr, 400 ml of tagged food was added. The animals were then allowed to feed on the hot mixture for 15 to 30 min. They were relaxed with CO_2 water, killed with boiling water, and preserved. Each experiment was run in quadruplicate. In the laboratory, animals were picked using a 1 mm diameter metal loop, carefully avoiding the removal of large filamentous algae. Approximately 50 animals were placed in a scintillation vial and digested with Protosol (New England Nuclear); after 24 hr at 60°C, the vials were filled with 10 ml of cocktail (49% toluene and 49% ethylene glycol monomethyl ether and 2% Liquifluor [NEN]). All samples were placed in the dark for 24 hr to eliminate chemoluminescence and then counted in a Beckman Model 133 liquid scintillation counter. Typically, zooplankton samples were counted with an efficiency of 95%, as contrasted to phytoplankton foods counted at 65% efficiency.

Samples of the natural phytoplankton assemblage of southern Lake Huron were collected at two nearshore stations, one near the outlet at Port Huron (Station 63) and one in the mouth of Saginaw Bay (Station 47). Samples of the natural zooplankton community were taken by a vertical tow (0 to 5 m) using a net of 64 μm aperture at these close-by stations (Fig. 1) (Table 1).

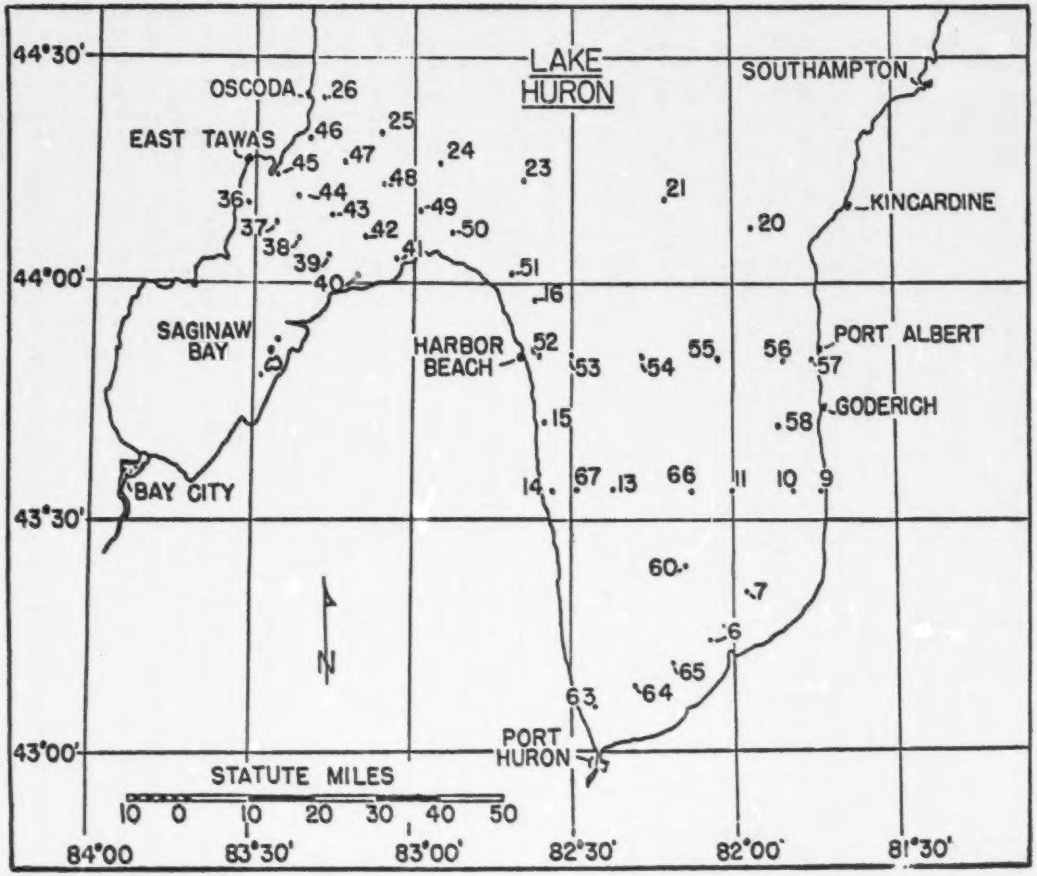
LAKE HURON
OSCODA
EAST TAWAS
SAGINAW BAY
BAY CITY
HARBOR BEACH
PORT HURON
SOUTHAMPTON
KINCARDINE
PORT ALBERT
GODERICH
26
25
46
47
24
45
48
23
21
44
43
49
42
50
20
36
37
38
39
40
41
51
16
52
53
54
55
56
57
58
15
14
67
13
66
11
10
9
60
7
6
65
64
63
N
STATUTE MILES
10 0 10 20 30 40 50
44°30'
44°00'
43°30'
43°00'
84°00
83°30'
83°00'
82°30'
82°00'
81°30'

Figure 1. Map of station locations in Southern Lake Huron.

TABLE 1. CRUISE SCHEDULE(A) AND STATIONS(B) CONSIDERED WITHIN WATER QUALITY MANAGEMENT AREAS (4-10)

A.

Cruise Number	Cruise Dates
11	April 28-May 3, 1974
12	May 14-17, 1974
13	June 04-08, 1974
14	June 16-21, 1974
15	July 17-22, 1974
16	August 26-31, 1974
17	October 08-12, 1974
18	November 10-14, 1974
20	April 02-13, 1975
21	May 28-31, 1975
22	August 06-10, 1975
23	October 17-23, 1975

B.

Area	Stations
Area 4	14, 15, 26, 46, 52, 63
Area 5	36, 37, 38, 39, 40, 41, 42, 43, 44, 45
Area 6	16, 23, 24, 25, 47, 48, 49, 50, 51, 53, 67
Area 7	6, 64, 65
Area 8	7, 9, 10, 56, 57, 58
Area 9	11, 13, 54, 55, 60, 66
Area 10	20, 21

4.2 METHODS FOR FIELD STUDIES OF SELECTIVE GRAZING

Techniques similar to the above for total grazing were employed, except that food resources were size-fractionated. The natural assemblage of phytoplankton was passed through a fine net (22 μm), leaving the nannoplankton (< 22 μm) in the lakewater and removing the netplankton (> 22 μm), which was resuspended in filtered (0.45 μm) lakewater. Tagged (^{14}C) nannoplankton, following a 4 hr *in situ* incubation, were mixed with cold netplankton to reconstitute the natural assemblage. In a similar manner, tagged netplankton were mixed with cold nannoplankton just before feeding. The natural assemblage of herbivores, already acclimated to their food assemblage, was reacclimated for 1 hr in watercooled shipboard tanks. Animals acclimated in 400 ml lakewater were fed 600 ml hot food. After feeding for 12 to 15 min, the animals were killed and preserved.

Assimilation was calculated by feeding animals for 1 hr, as above, and then removing them and placing them in cold food for 4 hr, during which time any hot food would be eliminated from the gut. Assimilated food was measured as above, using liquid scintillation techniques. Percentage assimilation (Sorokin, 1968) was calculated from the ratio mgC assimilated hr^{-1} to mgC ingested hr^{-1}.

4.3 METHODS FOR LABORATORY STUDIES OF SELECTIVE GRAZING

Paired-food Selection Experiments

Seven common herbivorous crustaceans, including five adult stages (*Diaptomus sicilis*, *Cyclops bicuspidatus*, *Cyclops vernalis*, *Tropocyclops prasinus*, and *Eubosmina coregoni*) and two of their larval stages (copepod nauplii and cyclopoid copepodites), were fed mixtures containing 50% by volume one of two blue-green algae (*Gloeocapsa* sp., *Anacystis nidulans*) and one of three green algae (*Scenedesmus quadricauda*, *Ankistrodesmus falcatus*, and *Pediastrum* sp.). These experiments involved two treatments with replicates, one treatment in which the blue-green was tagged (50 μCi ^{14}C) and the green cold, and the other where the green algae was tagged (^{14}C) and the blue-green cold. A minimum of six internal replicates for each of these combinations were available. Thus, 24 independent treatments resulted in 144 samples containing 7 herbivores. Approximately two subsamples of 50 animals were picked by hand from each sample; thus, approximately 1×10^5 animals were handpicked to provide data on selective feeding at the species/stage level. Differences in selectivity were detected, using the t-statistic for unpaired means and a 2-level ANOVA. In addition, electivities were calculated according to the method of Ivlev (1955).

Bead Selection Experiments

Herbivorous zooplankters rely not only on size, but shape, taste, and other factors in selectively feeding. A food source characterized only by size would be of immense experimental use. We selected polystyrene beads which are sphaerical, tasteless, and vary in size. These specific beads were formulated by Dr. M. Gliwicz in the Laboratory of Hydrobiology at Warsaw University. They varied in size from 0 to 10 μm diameter, with a peak in frequency at 3 μm. Beads were mixed with the natural food assemblage on shipboard and fed to the natural zooplankton populations. After 30 min animals were relaxed and killed. The zooplankton were mounted in a Turtox medium (CMCP) and the beads measured under oil immersion, using a calibrated ocular disk. The bead population in the gut was then compared to that of the environment in determining selectivity and electivity.

4.4 METHODS FOR PLANKTON COLLECTION

The crustacean zooplankton were collected in a large cone net (0.8 m diameter, 3 m hang) of 64 μm aperture nitex. Hauls were made from 0 to 5 m, 0 to 10 m, 0 to 20 m, and 0 m to bottom at each survey station. Animals were concentrated and stored in buffered formalin. In the laboratory, animals were concentrated to 25 to 100 ml, and three 1 ml aliquots were counted. Enumeration for adults was to species and sometimes sex (diaptomid copepods). Immature copepods were lumped as nauplii and cyclopoid and calanoid copepodites.

4.5 METHODS FOR ACOUSTIC BIOMASS ESTIMATES

Large scale sampling to determine zooplankton biomass is expensive relative to vessel time required, and even more so with regard to processing samples. We have developed an acoustical technique for estimating the biomass of particulate organic material in suspension (McNaught, 1975). Estimates are normally categorized within three size classes (0.8 to 2 mm, 2 to 3 mm, 3 to 5 mm) by utilizing the increased signal return within envelopes created by the 500 and 200 kHz, 200 and 120 kHz, and 120 and 80 kHz frequency transmitter-receivers. This technique readily illustrates the distinct advantage of handling large amounts of data. However, acoustical methods have the disadvantage that targets, while placed into size categories, cannot as yet be classified by biological category (order, species, etc.).

SECTION 5

RESULTS

5.1 GRAZING BY ZOOPLANKTON UPON NATURAL PHYTOPLANKTON POPULATIONS: SEASONAL AND DIEL ESTIMATES OF TOTAL ZOOPLANKTON GRAZING

Formulations for Grazing Estimates

Students of the grazing process have traditionally relied upon two measures of grazing, the species or community filtering rate, and the community grazing rate. We will modify the second concept and add a third, the relative impact of grazing or the amount of productivity grazed.

Filtering Rate (F.R.)--

The most commonly used index of grazing is the filtering rate (Rigler, 1961). Actually filtering rates are backcalculated from ingestion rates, which all investigators measure. Using isotope (^{14}C) techniques, if the ratio of radioactive to cold cells in the feeding suspension is known, and the activity of animals is measured, ingestion can be calculated. But since ingestion efficiencies may vary from 0.5 to 2.0% (Bogdan and McNaught, 1975), actual filtering rates are higher than the minimal filtering rates calculated by most investigators from the following formulation:

$$\text{(I)}\quad FR = \frac{\text{Activity animals/No. animals}}{\text{(Activity phytoplankton/Volume phyto)} \times \%\ \text{hot} \times \text{time}}$$

$$= \frac{\text{cpm an}^{-1}}{\text{cpm ml}^{-1}\ \text{hr}} = \text{ml an}^{-1}\ \text{hr}^{-1}$$

Grazing Rates (G.R.)--

Once the minimum filtering rate has been determined, only the density of grazers must be known to calculate the grazing rate. Grazing rates have units of relative water volume grazed per time (% day^{-1}) or relative amount of algal carbon grazed per unit time (% day^{-1}). Both of these indices are useful, but since the grazing efficiency has often been ignored, those grazing rates based upon volume (IIA) may be less ecologically meaningful than those based on algal carbon grazed (IIB). In either case, they are calculated from a knowledge of filtering rates as follows:

(IIA) Based on water volume:

$$GR_{volume} = \frac{\text{No. animals x FR}}{\text{unit water volume}} = \frac{m^3\ day^{-1}}{m^3} = \%\ day^{-1}$$

(IIB) Based on carbon:

$$GR_{carbon} = \frac{\text{algal carbon ingested}}{\text{algal carbon available}} = \frac{(\%\ day^{-1})(mgCm^{-3})}{(mgCm^{-3})} = \%\ day^{-1}$$

Thus, the grazing rate involves the loss of carbon (dC) with regard to the standing crop (C), or the integral,

$$\frac{1}{C}\frac{dC}{dt}$$

Relative Grazing Impact (G.I.)--

In contrast to the grazing rate, we can express the amount of carbon grazed with regard to the amount fixed the same day by the primary producers. Immediately this notation tells us at what times the grazers are overharvesting the primary production. The impact upon productivity is calculated using the filtering rate (Eq. I), but the denominator is the rate of primary productivity (mgC m^{-3} hr^{-1}) instead of the standing crop of algal C (mgC m^{-3}), as in the grazing rate calculation. Impact on primary productivity is thus determined as follows:

$$\text{(III)}\quad G.I. = \frac{\text{algal carbon ingested}}{\text{algal carbon fixed}} = \frac{(\%\ day^{-1})(mgCm^{-3})}{(mgCm^{-3}\ day^{-1})} = \%$$

Note that the units (%) refer to the percentage of productivity (carbon fixed) which was grazed, where both the processes are calculated over the same time interval.

In contrast to the grazing rate, this measure of the impact of grazing on primary productivity involves the integral of change (decrease) in plant carbon with time, due to ingestion by zooplankton, divided by the integral of the change (increase) in plant carbon fixed with time, where:

$$\frac{\int_{t_0}^{t_1} dC/dt}{\int_{t_0}^{t_1} dC/dt}$$

If all the species of G.I. terms are summed, we have the total community grazing impact (C.G.I.) discussed later in this section.

Grazing Budgets

Monthly Budgets--

Grazing budgets have been compiled for each monthly cruise on Southern Lake Huron. Three basic indices have been employed, including the filtering rate (Eq. 1) for each species, life stage, and the total community; the grazing rate (Eq. 2b) based on carbon, and the percentage of gross primary production (GPP) grazed (Eq. 3) both during daylight and darkness. Detailed budgets have been provided for periods of limited grazing, including August 1974 (Table 3), as well as periods of intense grazing during July 1974 (Table 2) and November 1974 (Table 4).

During July 1974, the relatively rare Holopedium gibberum constituted only 1.4% of the crustacean density, but due to a high filtering rate (0.416 ml an^{-1} hr^{-1}) and high ratio of food intake per unit biomass, it accounted for 26.2% of the C grazed (Table 2). The most important grazers were the calanoid copepods (69.5% numbers), which did 60.5% of the grazing. Abundant copepod nauplii (63906 m^{-3}) (5.2%) and the cyclopoid copepodites (16369 m^{-3}) (5.8%) were a distant third and fourth respectively. As expected, relatively little grazing was done by rare species which constituted an insignificant percentage of total zooplankton biomass. Bosmina longirostris (0.3% numbers) contributed only 0.7% grazing, while Tropocyclops prasinus, a small cyclopoid (0.8% numbers), contributed only 0.2% grazing.

Grazing was greatly depressed during August 1974. The most abundant organisms, the calanoid copepodites (35.2% numbers), accounted for 26.5% grazing during daylight, as opposed to 0.3% during darkness. Copepod nauplii, second in abundance (29.7% numbers), by virtue of higher filtering rates at night, did 49.5% grazing during daylight and 62.0% at night. Diel differences in grazing are significant. Most grazing is accomplished with populations feeding nearer the surface at night.

Grazers actually overcropped phytoplankton production (GPP) during October 1974 (Table 5). During daylight, abundant calanoid copepodites (26.3% numbers), although characterized by low filtering rates (.005 ml an^{-1} hr^{-1}), did 39.9% of the grazing; nauplii grazed 18.5% of GPP to account for much of the remainder. However, Daphnia galeata (6.6% numbers), with a high filtering rate (.059 ml an^{-1} hr^{-1}), and Epischura lacustris (6.0% numbers), with a very high filtering rate (.526), accounted for 5.2 and 12.6% of the grazing, respectively. October was the only month other than April when an adult calanoid (Epischura) accounted for more than 10% of grazing during daylight. Adult calanoids must be chiefly predatory in nature. In contrast, grazing was slightly increased during hours of darkness. Again calanoid copepodites, with greatly increased filtering rates (0.414), did most (38.5%) of the grazing, followed by the nauplii (17.2%) and Holopedium gibberum (10.4%). Also, in October a large number of minor forms were important. Bosmina longirostris and Eubosmina coregoni both exhibited high filtering rates during day and night, as did Daphnia retrocurva.

TABLE 2. GRAZING BUDGET FOR DAYTIME, 23-26 JULY 1974, FOR SOUTHERN LAKE HURON

Species and Stage	Filtering Rate $ml\,an^{-1}hr^{-1}$	Grazing Rate $\frac{C\ grazed}{C\ algal}$ % day^{-1}	%N. Primary Prod. Grazed $\frac{C\ grazed}{C\ fixed}$ %
Cladocera		Daytime	
Eubosmina coregoni	0.072	1.71×10^{-5}	1.36×10^{-5}
Bosmina longirostris	0.072	2.11	1.69
Daphnia retrocurva	0.010	3.30	2.60
Holopedium gibberum (A + J)	0.416	63.4	50.0
Polyphemus pediculus	0.038	0.2	0.20
Leptodora kindtii	0.006	0.04	0.04
Copepoda			
Nauplii	0.002	12.76	10.00
Diaptomus (A)	0.090	0.85	0.68
Diaptomus (C)	0.090	147.3	115.9
Cyclops bicuspidatus (A)	0.005	1.15	0.91
Cyclops bicuspidatus (C)	0.005	14.22	11.20
Tropocyclops prasinus	0.005	0.50	0.40
TOTAL	0.021	0.25% hr^{-1} or 6.0% day^{-1}	0.19%

TABLE 3. GRAZING BUDGET FOR DAYTIME AND NIGHTTIME, 26-30 August 1974, FOR SOUTHERN LAKE HURON (A = ADULT, J = JUVENILE, C = COPEPODITE)

Species and Stage	Filtering Rate (±S.E.) $mlan^{-1}hr^{-1}$	Grazing Rate $\frac{C\ grazed}{C\ algal}$ % day^{-1}	%N. Primary Prod. Grazed $\frac{C\ grazed}{C\ fixed}$ %	Filtering Rate (±S.E.) $mlan^{-1}hr^{-1}$	Grazing Rate $\frac{C\ grazed}{C\ algal}$ % day^{-1}	%N. Primary Prod. Grazed $\frac{C\ grazed}{C\ fixed}$ %
Cladocera		Daytime			Nighttime	
Eubosmina coregoni	0.013 ± .009	1.46×10^{-5}	0.22×10^{-5}	0.0005 ± .0004	1.34×10^{-5}	0.21×10^{-5}
Bosmina longirostris	0.004 ± .001	0.48	0.08	0.0001	0.36	0.05
Daphnia retrocurva	0.010 ± .004	0.10	0.015	0.0016	0.36	0.01
Daphnia galeata (A)	0.059 ± .047	0.43	0.07	0.00069	0.12	0.02
Daphnia galeata (J)	0.059 ± .047	0.43	0.07	-	-	-
Holopedium gibberum (A)	0.010 ± .002	0.76	0.12	0.0016 ± .0013	2.90	0.44
Holopedium gibberum (J)	0.016 ± .008	0.76	0.12	0.0032 ± .0028	0.60	0.09
Polyphemus pediculus	0.015 ± .003	0.09	0.13	-	-	-
Leptodora kindtii	0.006 ± -	0.05	0.01	-	-	-
Copepoda						
Nauplii	0.002 ± -	15.48	2.33	0.002	66.90	10.08
Diaptomus (A)	0.005 ± .001	1.10	0.17	0.0005 ± .0004	2.8	0.42
Diaptomus (C)	0.005 ± .001	8.17	1.25	0.0001	0.36	0.06
Cyclops bicuspidatus (A)	0.004 ± .001	0.06	0.01	0.004	1.40	0.23
Cyclops bicuspidatus (C)	0.003 ± .001	1.24	0.19	0.003 ± .003	29.70	4.48
Tropocyclops prasinus	0.005 ± -	0.003	0.06	0.005	5.90	0.92
TOTAL	0.005	0.03% hr^{-1} or 0.74% d^{-1}	0.005%	0.0009	0.11% hr^{-1} or 2.7% d^{-1}	0.027%

TABLE 4. GRAZING BUDGET FOR DAYTIME, 10 NOVEMBER 1974, FOR SOUTHERN LAKE HURON

Species and Stage	Filtering Rate $mlan^{-1} hr^{-1}$	Grazing Rate $\frac{C\ grazed}{C\ algal}$ $\%\ day^{-1}$	%N. Primary Prod. Grazed $\frac{C\ grazed}{C\ fixed}$ %
Cladocera		Daytime	
Eubosmina coregoni	0.082	0.330×10^{-4}	0.078×10^{-2}
Bosmina longirostris	0.003	0.001	0.003
Daphnia galeata (A)	0.035	0.416	0.097
Holopedium gibberum (A)	0.019	0.106	0.025
Copepoda			
Nauplii	0.002	0.081	0.023
Diaptomus (A)	0.012	0.312	0.088
Diaptomus (C)	0.001	0.086	0.024
Cyclops bicuspidatus (A)	0.008	0.021	0.006
Cyclops bicuspidatus (C)	0.001	0.071	0.020
Tropocyclops prasinus	0.002	0.001	0.0004
TOTAL	0.005	$0.04\%hr^{-1}$ or $1.06\%d^{-1}$	0.36%

Summary: Important Species and Stages by Month

Limnocalanus macrurus and nauplii of copepods (probably a large percentage calanoid nauplii), as well as a few adults of *Diaptomus sicilis*, were the important grazers under the slush ice on 2 April (Figure 2). This is not surprising, since *Limnocalanus* is adapted to waters below 11°C (McNaught, 1966) and exhibits its highest filtering rates at 0.6°C (Figure 4), as discussed later. By 5 May, copepod nauplii were totally dominant, although *Diaptomus sicilis* was still important and *Holopedium* had made its first contribution to grazing. By late July, calanoid copepodites, most likely those developed from the previously dominant nauplii, significantly increased grazing, along with *Holopedium* (Table 2). Grazing plummeted during August (Table 3). The small amount of production was grazed by nauplii (mostly cyclopoids) and a decreasing population of calanoid copepodites, *Diaptomus minutus* and *D. ashlandi*, *Holopedium*, *Daphnia galeata*, *Bosmina longirostris* and *B. coregoni*. Thus, the month of least grazing pressure was 1) the month of greatest zooplankton density, and 2) the month of greatest zooplankton diversity. In October, when grazing was influential in reducing the amount of primary production, zooplankton such as nauplii, calanoid copepodites, cyclopoid copepodites, *Bosmina*, and *Epischura lacustris* were important. By November, *Daphnia galeata* and *Epischura* had increased in importance at the expense of the developmental stages of copepods.

Impact of Grazers upon Carbon Pool

The standing crop of algal carbon was greatest during April 1975 and October 1974, although the flux to this pool through primary production (GPP) was largest in July 1975 and August 1975 (Table 5). This fixation (GPP) of carbon by the algae was the only flux into the pool. Grazing upon the algae by zooplankton, a major loss from the pool, was greatest in July and especially October 1975 when carbon grazed was over one-third the carbon fixed (Figure 3, Table 5). Thus, high fixation rates and negligible grazing during August were at least in part responsible for higher standing crops of phytoplankton in October. In a similar fashion, since grazing of C exceeded fixation during October, standing crops showed a reduction in November (Table 4).

Controls upon Grazing

Temperature, Filtering, and Ingestion Rates--

At first analysis, both low and high water temperatures apparently inhibit filtering rates and thus the ingestion of algal C by the dominant cladocerans and copepods and their immature life stages in Lake Huron (Figure 4). In analyzing this figure and all the remaining figures throughout this report, the

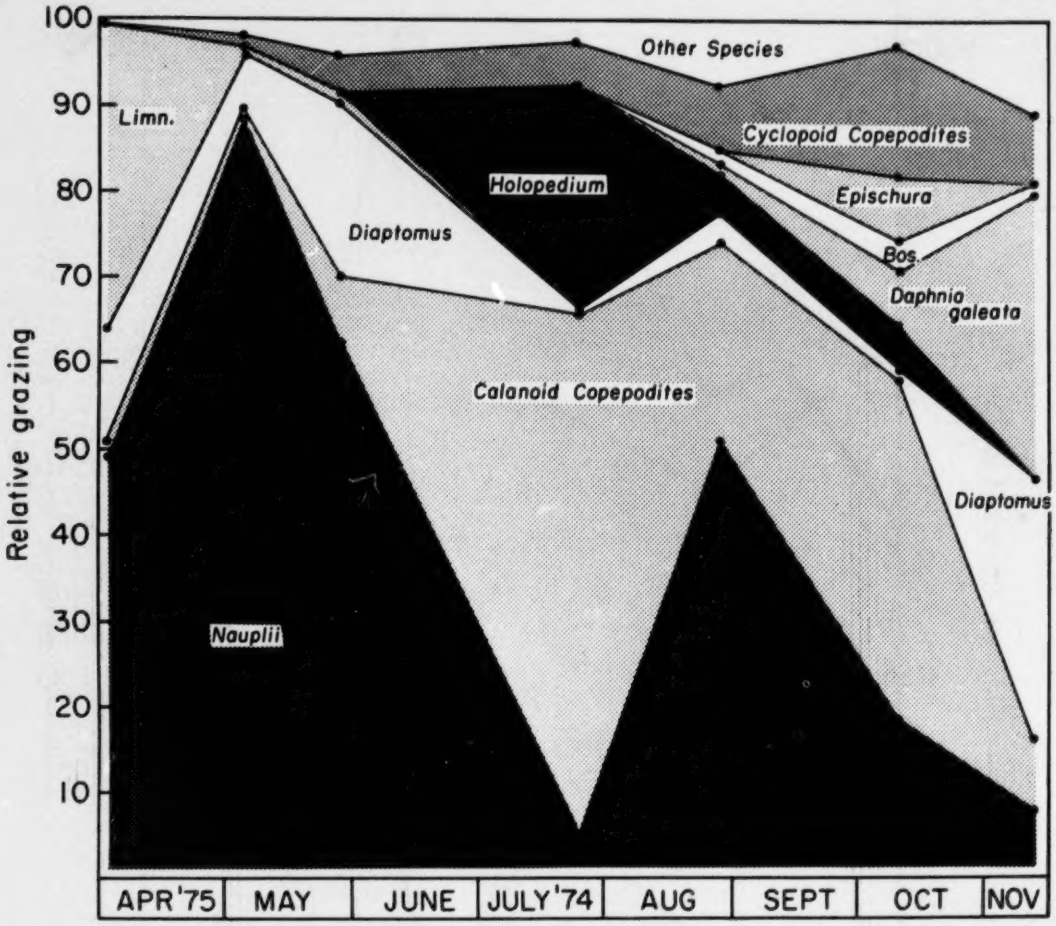

Figure 2. Relative contribution to total phytoplankton grazing by important species and life stages of crustacean zooplankton in Southern Lake Huron (Limn.:Limnocalanus; Bos.:Bosmina longirostris).

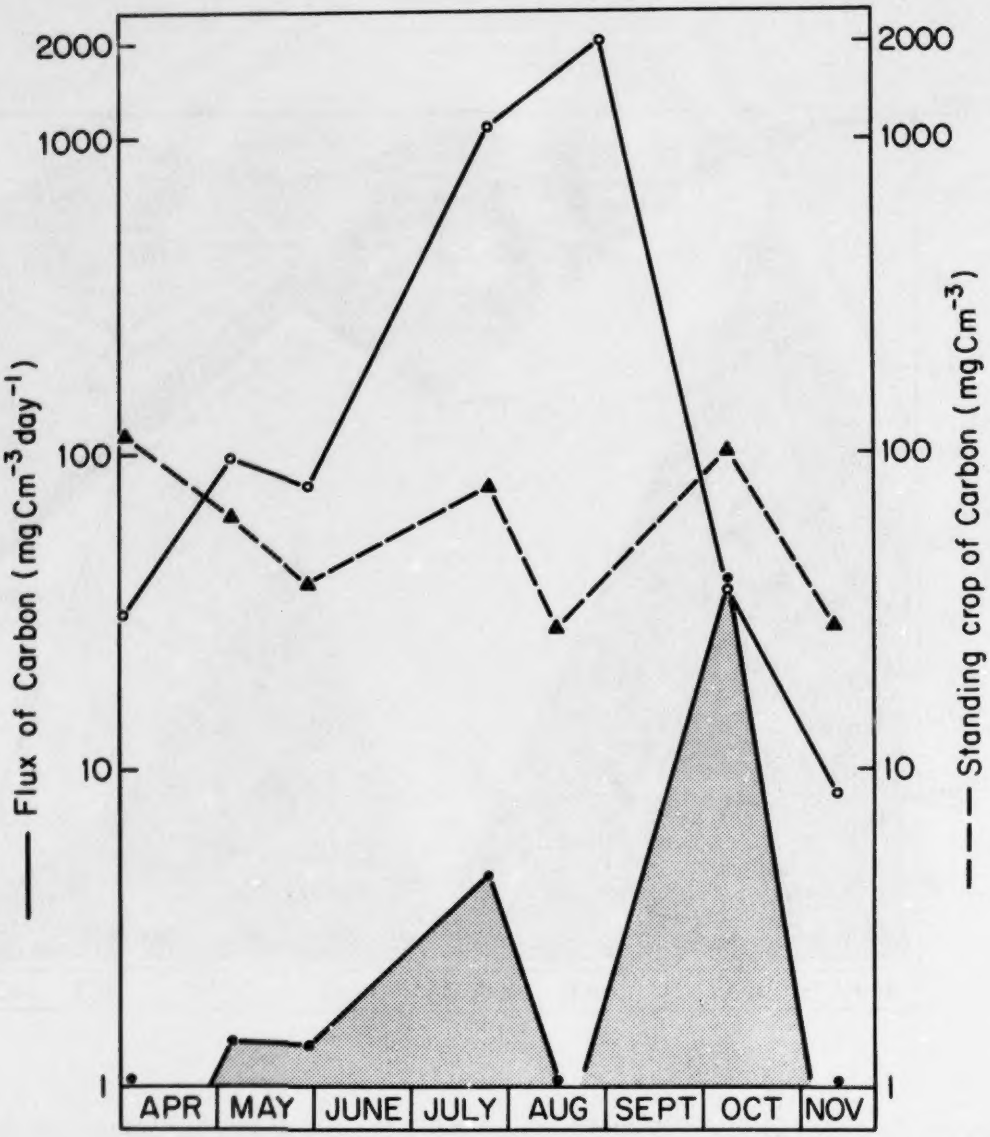

Figure 3. Phytoplankton (as carbon) grazing rate by crustacean zooplankton contrasted to standing crop of phytoplankton carbon and rate of fixation of carbon by phytoplankton in Southern Lake Huron.

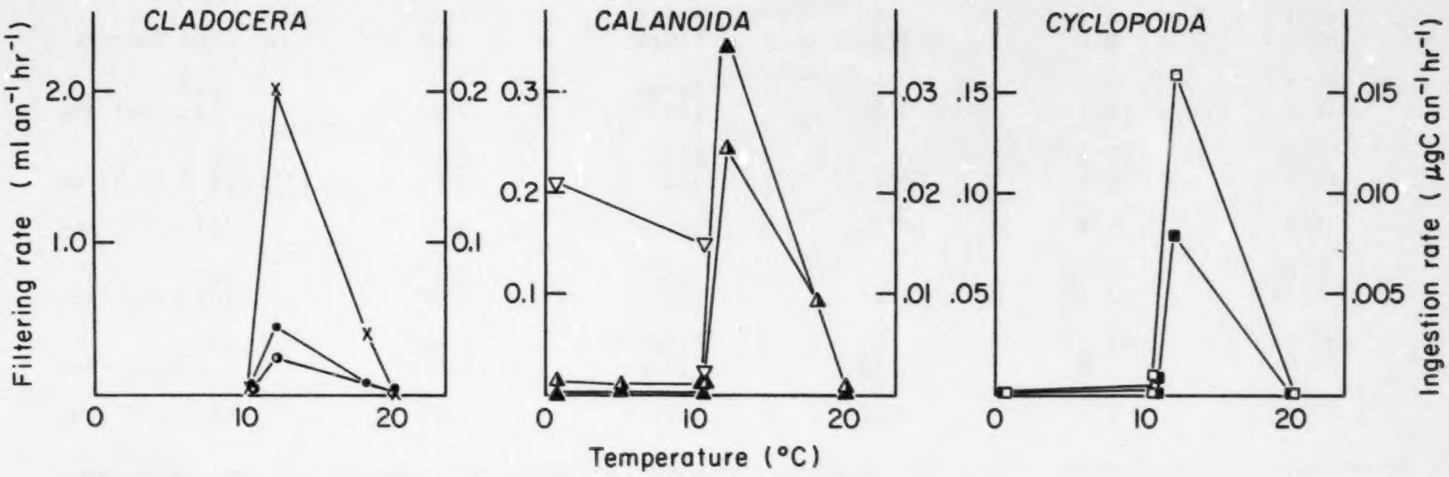

Figure 4. Filtering and ingestion rates of common crustacean zooplankton relative to water temperature.

TABLE 5. COMMUNITY FILTERING RATE, NET PRIMARY PRODUCTIVITY (NPP), GRAZING RATE AND RATIO OF CARBON GRAZED:CARBON FIXED, DURING DAYTIME AND NIGHTTIME FOR CRUISES ON SOUTHERN LAKE HURON D = DAYTIME, N = NIGHTTIME)

Date of Cruise	Community Filtering Rate (ml an^{-1} hr^{-1})	Zooplankton Density (no/m^3)	NPP (mgCm^{-3}hr^{-1})	Grazing Rate $\frac{\text{C grazed}}{\text{C algal}}$ (% day^{-1})	% NPP Grazed $\frac{\text{C grazed}}{\text{C fixed}}$ (%)
July 1974 (D)	.021	115626	100.0	6.0	0.19
Aug. 1974 (D)	.005	47112	191.5	0.7	0.13
(N)	.001	47112	-	2.70	0.048
Oct. 1974 (D)	.248	61761	4.7	36.7	33.2
(N)	.281	61761	-	41.9	37.8
Nov. 1974 (D)	.004	30103	1.2	0.3	0.3
April 1975 (D)	.010	2725	3.1	0.07	0.09
(N)	.032	2725	-	0.21	0.31
May 1975 (D)	.007	79941	9.1	1.3	0.37
(N)	.022	79941	-	3.4	1.00
May-June 1975 (D)	.008	47543	7.3	0.8	0.19
(N)	.067	47543	-	7.7	1.72

following species' codes will be necessary:

Holopedium gibberum (A) = ⊗
Daphnia galeata (A) = ○
Chydorus sphaericus = ◑
Eubosmina coregoni = ◐
Bosmina longirostris = ●

Cyclopoid cops. = ■
Cyclops vernalis = ⊠
Cyclops bicuspidatus = □

nauplii = △
Calanoid cops. = ▲
Diaptomus (A) = ◮
Limnocalanus = ▽

Filtering rates were maximum for the cladocerans at 12°C, with adults of *Daphnia galeata* and *Bosmina longirostris* filtering below 0.5 ml an^{-1} hr^{-1}. Calanoid copepods presented a similar pattern, with the important exception of *Limnocalanus macrurus*. *Diaptomus* adults exhibited maximum rates of 0.24 ml an^{-1} hr^{-1}, while their copepodites were typically 58% higher (0.38). For both, filtering was negligible at 0.6, 5, 10, and 20°C. *Limnocalanus*, the largest calanoid copepod in the Great Lakes and a stenothermal relict specie occupying cold hypolimnetic waters during summer months, exhibited a distinct pattern of temperature response. Filtering rates were highest at 0.6°C under slush ice and decreased at 10°C, most likely an adaptation to its unusually cold environment.

The rate of ingestion of algal carbon by zooplankton (mgC an^{-1} hr^{-1}) showed a similar pattern, which was expected because filtering rates are determined from measurements of ingestion (Figure 4). From the viewpoint of community trophic dynamics, it should be noted that the relatively small *Bosmina longirostris* had a higher maximum ingestion rate than *Daphnia galeata*, at about twice its biomass. Likewise, ingestion rates of calanoid copepodites exceeded those of adult *Diaptomus* and even the large *Limnocalanus*. Maximum ingestion rates for *Cyclops bicuspidatus* and cyclopoid copepodites were lower than those of the calanoids and cladocerans; cyclopoids are probably omnivorous, relying less upon plant foods.

The low optimum temperature for feeding (12°C) was not surprising. The mean temperature (April-November) for the waters (upper 10 meters) of Lake Huron is approximately 13°C. However, significant inhibition of feeding at 10 and 20°C most likely occurs as a result of factors other than temperature, as discussed below.

Effects of Food Concentration--

McMahon and Rigler (1961) discovered a saturation feeding level of 10^5 cells/ml (yeast) for large *Daphnia magna*; ingestion was constant at food levels higher than this. *Diaptomus oregonensis* exhibits a similar level (Richman, 1966). Recent examination of saturation feeding suggests that such rectilinear models are suitable, although saturation levels vary by species and may be as low as 10^3 cells/ml for the marine calanoid, Calanus (Frost, 1975). Plotting ingestion rates (mgC an^{-1} d^{-1}) against algal concentration (mgC m^3) suggested that important grazers like Diaptomus, as well as the entire natural community in Lake Huron, do not exhibit saturation feeding at algal carbon levels of $1x10^2$ mgC m^{-3} (Figure 5). For Lake Huron, this level of organic C corresponds to about $2x10^4$ algal cells per ml.

Grazing Versus Age Structure and Food Quality - Use of Mass Ingestion Rates--

The grazing effectiveness of a species or life stage is best illustrated by calculating the ratio of algal carbon ingested to unit body carbon (mgC d^{-1} mgC^{-1}). This mass ingestion rate, if unity, indicates that a species ingested algal carbon equivalent to its own body carbon in one day (similar to ingesting its own weight per day). Both seasonal and taxonomic trends are evident in these data (Figure 6).

The seasonal range of this ingestion ratio varied from 8.5×10^{-4} mgC d^{-1} mgC^{-1} for Limnocalanus adults in May to 1.8×10^0 for copepod nauplii in October. That is, Limnocalanus daily ingested algal C equivalent to 0.09% of its body C which is equal to 180% of their body carbon in October. This ingestion ratio in effect provides an index to the efficiency of utilization of the phytoplankton stock by zooplankton. Seasonally, three periods of greatly reduced ingestion, where all species and life stages show reduced intake, are evident; these are late May during the diatom bloom, late August during the blue-green bloom, and November during the fall diatom pulse.

Two factors of physiological importance may be basic to the limitation of ingestion. Many species of zooplankton have specific size preferences. For example, Diaptomus prefers small algal cells (< 22 µm) and others such as Daphnia feed non-selectively over a wide range of sizes (Bogdan and McNaught, 1975). Thus, when large algal cells are abundant, the animals must shift to larger forms, select rare small species in low density, or shift to non-algal foods. Apparently, during late May and June, when the majority of algal cells are diatoms (92.5%) and mostly large (Table 6), these populations of crustaceans turned to other foods. Certainly they did not consume those species which had fixed ^{14}C, as indicated by the low ratio of algal C ingested to body C.

Secondly, the antibiotic or inhibitory nature of algal metabolic products has been extensively investigated, beginning with the experiments of Ryther (1954) and continuing today. During August, the Cyanophyta or blue-green algae were abundant in the open lake (76% biomass) (Table 6). While many small forms were present (Chroococcus, Gloeocystis), algal toxins and food size combined with other factors may have been responsible

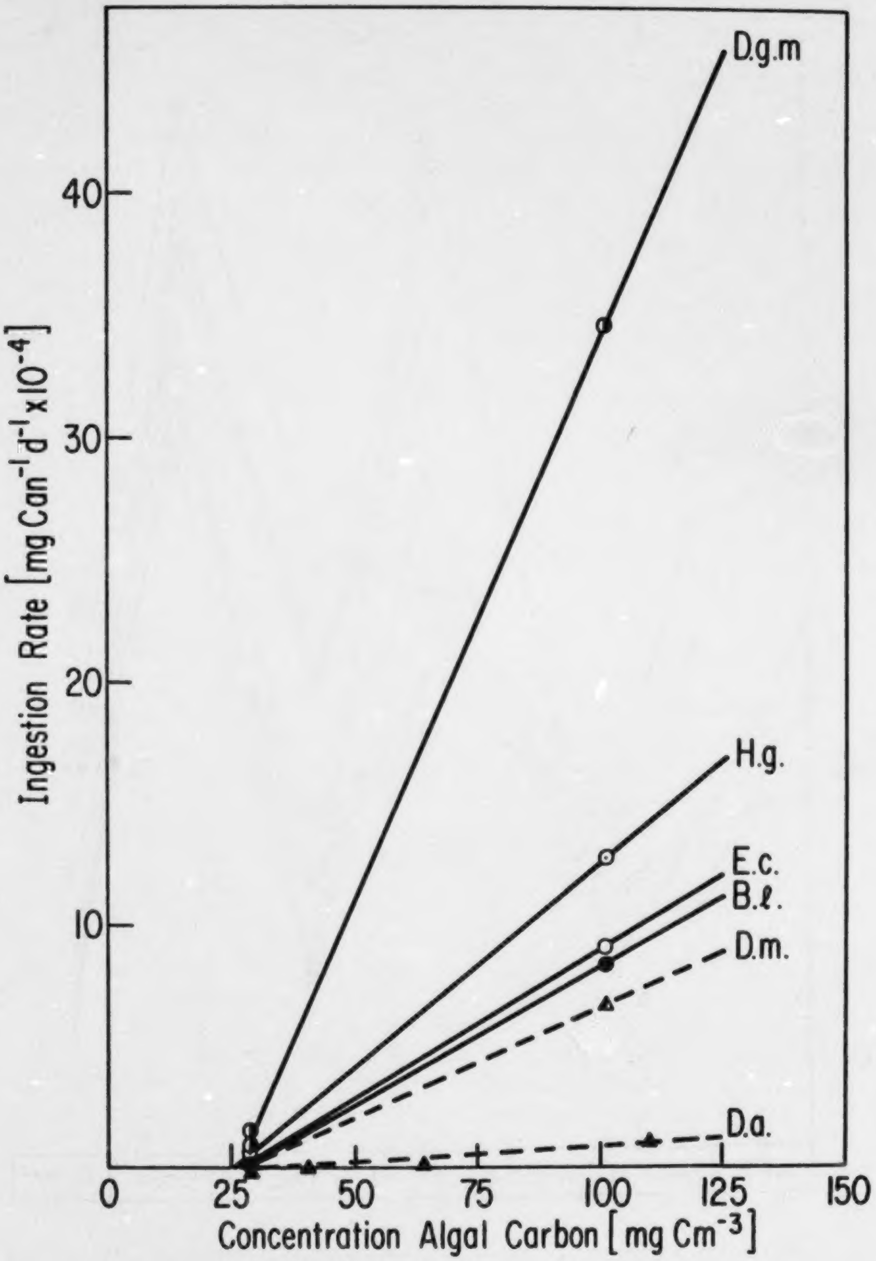

Figure 5. Ingestion rate of zooplankton species relat to food concentration in oligotrophic waters of Southern Lake Huron.

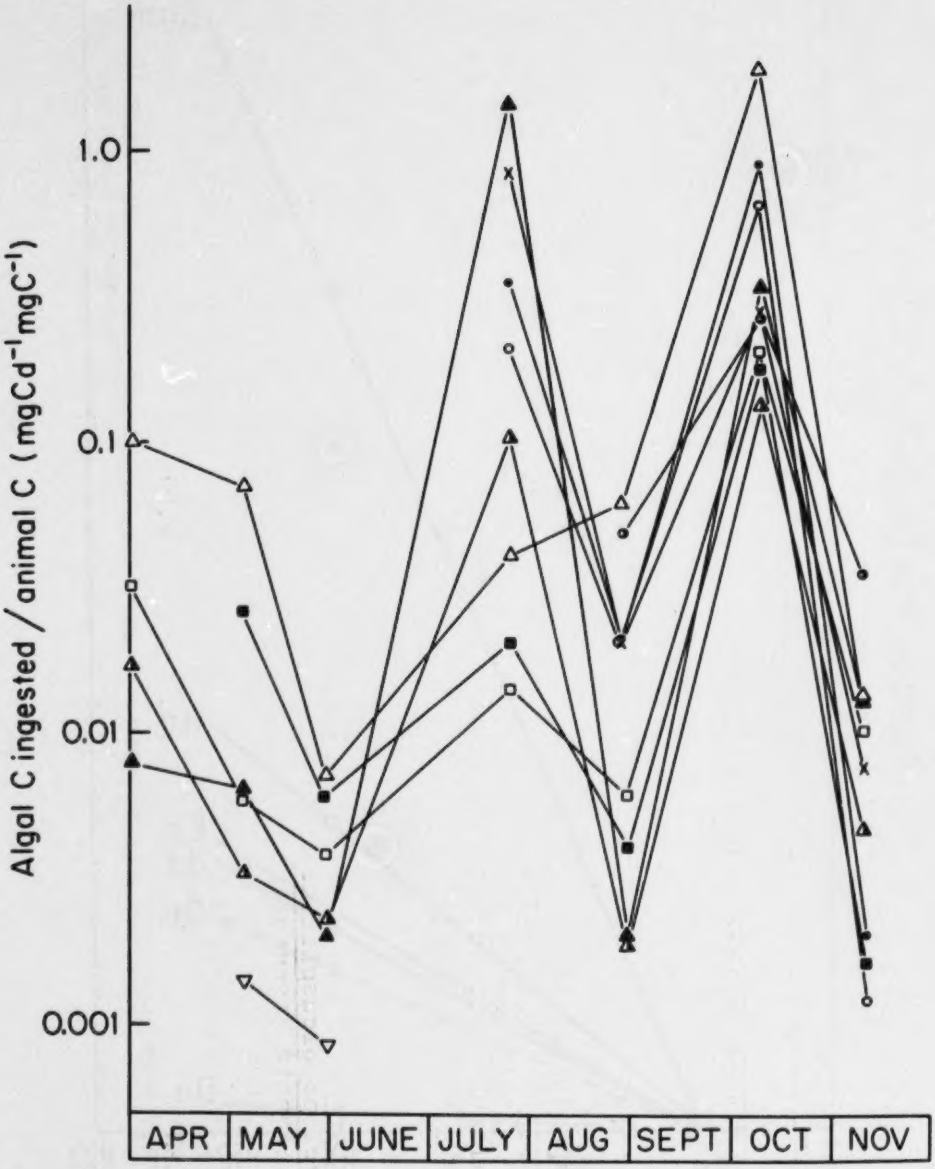

Figure 6. Mass ingestion rates of dominant zooplankton species by season (symbols in text).

TABLE 6. RELATIVE BIOMASS (% VOLUME) OF DIATOMS (BACILLARIOPHYTA) AND BLUE-GREEN ALGAE (CYANOPHYTA) AT FEEDING STATIONS IN SOUTHERN LAKE HURON IN 1974 (FROM STOERMER, 1978)

Functional Classification & Species or Stage	Mass Ingestion Rate ($mgCd^{-1}mgC^{-1}$) Mean	Range
Fast Ingestors		
Copepod nauplii	0.40	0.01 - 1.80
Daphnia galeata	0.32	0.25 - 0.37
Bosmina longirostris	0.30	0.01 - 0.85
Holopedium gibberum	0.27	0.01 - 0.80
Calanoid copepodites	0.25	0.001- 1.44
Eubosmina coregoni	0.21	0.001- 0.62
MEAN	0.29	
Slow Ingestors		
Cyclops bicuspidatus	0.05	0.005- 0.19
Cyclopoid copepodites	0.04	0.002- 0.17
Diaptomus spp.	0.04	0.002- 0.13
Limnocalanus macrurus	0.01	0.008- 0.015
MEAN	0.04	

for reduced ingestion (Figure 4). Certainly temperature was not the cause of decreased feeding.

Species trends were evident regarding the rate of C ingested during any month. Within taxonomic groups, the cladocerans exceeded the calanoid and cyclopoid copepods. However, larval calanoids (copepodites) and nauplii were often the fastest ingestors (Figure 6). Over the growing season, from April through November, two or three groups of organisms were evident, based on their rate of ingestion of algal C (Table 7). These have been termed fast ingestors (greater than 21% body weight per day) and slow ingestors (less than 5% body weight ingested per day). Fast ingestors are most likely herbivores, whereas slow ingestors are omnivores or carnivores. For the first time we have identified the trophic position of all of the crustaceans in the Lake Huron ecosystem.

Assimilation of Ingested Phytoplankton

In modeling the dynamics of ecosystems of the Great Lakes, not only is the rate at which phytoplankton is ingested important, but also the relative amount which is ultimately assimilated. Obviously the assimilated component leads to growth; the remainder is in part egested or remineralized. Cladocerans, copepod nauplii and copepodites showed the highest mass ingestion rates (Figure 6). If a species or life stage combines high ingestion with high assimilation, growth should be rapid.

Assimilation was highest for nauplii and cyclopoid copepodites (Table 8). These immature forms assimilated 53-55% of the food they ingested on a diel basis. It was necessary to measure assimilation both day and night, since feeding rates vary greatly on a diel basis. Since nauplii may ingest 180% of their body weight and assimilate 50% of this or 90% of their weight, they can double their size in a day, truly an example of "r-selection" growth characteristic of the zooplankton. Thus, we now have critical evidence, not only for fluxes of C into zooplankton but also for the assimilation of C, vital to modeling efforts on Great Lakes ecosystems.

5.2 GRAZING BY ZOOPLANKTON ON NATURAL ASSEMBLAGES OF NETPLANKTON AND NANNOPLANKTON

Grazing budgets on nanno- and net-plankton were calculated for each of six cruises on Southern Lake Huron (October, 1974; 12 April, 1975; May, 1975; 28 May - 2 June, 1975; 5 August, 1975; and 19 October, 1975). Budgets were determined for both daylight and nighttime feedings, since the amount of food grazed has been shown to vary cyclically throughout the day and is usually higher during the hours of darkness (Haney and Hall, 1975).

TABLE 7. MEAN AND RANGE OF ALGAL INGESTION RATES BASED ON MASS ($mgCd^{-1}mgC^{-1}$) FOR ZOOPLANKTONIC CRUSTACEANS OF SOUTHERN LAKE HURON

Class	17-18 June	24-26 July	12-14 Aug.	6-8 Oct.
Diatoms	92.5	50.1	15.8	83.4
Blue-greens	3.5	25.2	76.6	10.4

TABLE 8. ASSIMILATION AS PERCENTAGE OF TOTAL ALGAL CARBON INGESTED BY VARIOUS CRUSTACEANS

Species or stage	5 May 1975		28 May 1975		
	Daytime	Nighttime	Daytime	Nighttime	Mean
Calanoida					
Nauplii	-	-	100.	6.5	53.
Calanoid copepodites	54.5	-	71.7	11.4	46.
Diaptomus (A)	27.5	100.	13.0	0.9	46.
Limnocalanus macrurus	0.5	-	-	-	0.5
Cyclopoida					
Cyclopoid copepodites	14.0	100.	100.	6.3	55.
Cyclops bicuspidatus(A)	20.1	103.5	14.3	0.6	34.

Estimates of standing crops of both nannoplankton and netplankton were necessary to make grazing computations. These were determined from counts and cell volumes for each species of phytoplankton, which were kindly provided by Dr. E. Stoermer of the University of Michigan (Table 9).

Each budget (Table 10-17) separates the herbivorous zooplankton into the Cladocera and Copepoda. The cladocerans are further listed by species, and in the case of Holopedium gibberum and Daphnia galeata, by age (juvenile or adult). Adults were invariably parthenogenic females with eggs, or in very unusual cases, males. The remainder of the cladocerans were lumped by species and included all age groups which were present. The copepods were treated somewhat differently. All nauplii were treated as a group. The calanoids were classified generally as copepodites and specifically as adults by species. The cyclopoids were grouped as copepodites and adults of four prominent species (3 genera). Thus for many groups, information on selective grazing is available at both the immature and adult level for a number of species.

During October 1974, the nauplii of all copepods and the calanoid copepodites were the most active grazers. The nauplii grazed 25.3% of the nannoplankton productivity (25.3% during daylight and none at night), while the calanoid copepodites grazed 83.9% (61.3% during daylight and 22.6% at night). The only other important grazer on nannoplankton was Holopedium gibberum, which grazed 39.9% of the nannoplankton productivity (36.6% during daytime and 3.3% during nighttime). The crustacean community thus harvested 231.2% of the daily nannoplankton productivity (157.6% during daylight and 73.6% at night). In contrast, they grazed 78.4% d^{-1} (53.5% d^{-1} during daytime and 24.9% d^{-1} at night) of the nannoplankton standing crop. These figures illustrate how the zooplankton community may take over 100% of the productivity, but less than 100% of the standing crop. More importantly, at these exceptionally high grazing rates, it is obvious that the nannoplankton would be depleted below threshold grazing levels within a few days. As we will see later, during October, 1975 the nannoplankton was nearly depleted (only 56.9% mg Cm^{-3}) when observed.

During October 1974, the netplankton were not as severely grazed as the nannoplankton. Calanoid copepodites were the principle active grazers, exceeding the harvest of netplankton accomplished by all other forms. Calanoid copepodites harvested 45.2% of the netplankton productivity (13.1% during daytime and 32.1% at night). Epischura (9.8%) and Holopedium (10.4%) were important only during daylight hours. The zooplankton thus grazed 94.9% of the netplankton productivity (52.5% in daylight and 42.7% at night). Thus, from a productivity viewpoint, they were not quite in control of netplankton standing crops. In

TABLE 9. STANDING CROPS (mgCm^{-3}) OF NANNOPLANKTON (< 22 µm) AND NETPLANKTON (> 22 µm) USED IN CALCULATIONS OF PERCENTAGE CARBON GRAZED (CALCULATED FROM STOERMER ET AL. 1978)

Date of observation	Nannoplankton			Netplankton		
	Diatoms	Other	Total	Diatoms	Other	Total
3 May 1974	51.2	20.0	71.2	0	0	0
17 May 1974	36.2	37.8	69.0	0	0	0
8 June 1974	24.9	68.7	93.6	0	10.5	10.5
21 June 1974	71.7	13.9	85.6	0	0	0
22 July 1974	12.1	11.7	23.8	0	39.4	29.4
29 Aug. 1974	12.6	1020.0	1032.6	10.1	63.7	73.9
8 Oct. 1974	17.1	34.6	51.7	50.6	0	50.6
12 Nov. 1974	61.3	115.6	176.9	5.1	0	5.1

TABLE 10. GRAZING BUDGET ON NANNOPLANKTON, 12 APRIL 1975

	Daytime			Nighttime		
Species	Filtering Rate $ml\,an^{-1}hr^{-1}$	Grazing Rate $\frac{C\ grazed}{C\ part\text{-}algal}$ % day^{-1}	% Primary Prod. Grazed $\frac{C\ grazed}{C\ fixed}$ %	Filtering Rate $ml\,an^{-1}hr^{-1}$	Grazing Rate $\frac{C\ grazed}{C\ part\text{-}algal}$ % day^{-1}	% Primary Prod. Grazed $\frac{C\ grazed}{C\ fixed}$ %
Cladocera						
Eubosmina coregoni						
Bosmina longirostris						
Daphnia retrocurva						
Daphnia galeata (A)						
Daphnia galeata (J)						
Holopedium gibberum (A)						
Holopedium gibberum (J)						
Polyphemus pediculus						
Leptodora kindtii						
Chydorus sphaericus	.189±.156	9.53×10^{-4}	.281	.343*	17.23×10^{-4}	.508
Ceriodaphnia spp.						
Daphnia longiremis						
Copepoda						
Nauplii						
Diaptomus (A)	.215±.091	5.96	.175	—	—	—
Diaptomus (C)	.171±.117	5.17	.153	.665*	20.11	.593
Cyclops bicuspidatus (A)	.168±.056	3.60	.106	.135±.023	2.89	.085
Cyclops bicuspidatus (C)	.154±.086	49.50	1.461	.115*	36.97	1.091
Tropocyclops prasinus						
Limnocalanus macrurus	.712±.648	.21	.006	.576*	.17	.005
Cyclops vernalis						
Mesocyclops edax						
Epischura lacustris						
Eurytemora affinis						
TOTAL	.230	73.9×10^{-4} hr^{-1} or 17.8% d^{-1}	2.18 or 218.2%	.328	77.10×10^{-4} hr^{-1} or 18.5% d^{-1}	2.282 or 228%

TABLE 11. GRAZING BUDGET ON NETPLANKTON, 12 APRIL 1975

Species	Filtering Rate mlan^{-1}hr^{-1}	Grazing Rate $\frac{\text{C grazed}}{\text{C part-algal}}$ % day^{-1} Daytime	% Primary Prod. Grazed $\frac{\text{C grazed}}{\text{C fixed}}$ %	Filtering Rate mlan^{-1}hr^{-1}	Grazing Rate $\frac{\text{C grazed}}{\text{C part-algal}}$ % day^{-1} Nighttime	% Primary Prod. Grazed $\frac{\text{C grazed}}{\text{C fixed}}$ %
Cladocera						
Eubosmina coregoni						
Bosmina longirostris						
Daphnia retrocurva						
Daphnia galeata (A)						
Daphnia galeata (J)						
Holopedium gibberum (A)						
Holopedium gibberum (J)						
Polyphemus pediculus						
Leptodora kindtii						
Chydorus sphaericus	.030*	1.50x10^{-4}	.009	.058±.025	2.93x10^{-4}	.018
Ceriodaphnia spp.						
Daphnia longiremis						
Copepoda						
Nauplii	.008±.006	2.17	.014	-	-	-
Diaptomus (A)	.089±.018	2.47	.015	.048±.012	1.31	.008
Diaptomus (C)	.411±.239	12.42	.078	.225±.194	6.81	.043
Cyclops bicuspidatus (A)	.087±.051	1.85	.012	.032±.003	.68	.004
Cyclops bicuspidatus (C)	.022±.044	7.07	.044	.028±.016	9.00	.056
Tropocyclops prasinus						
Limnocalanus macrurus	-	-	-	.100*	.01	.000
Cyclops vernalis						
Mesocyclops edax						
Epischura lacustris						
Eurytemora affinis						
TOTAL	.098	27.48x10^{-4} hr^{-1} or 6.59%d^{-1}	.172 or 17.2%	.058	20.70x10^{-4} hr^{-1} or 4.99%d^{-1}	.129 or 12.9%

TABLE 12. GRAZING BUDGET ON NANNOPLANKTON, 5-9 MAY 1975

Species	Filtering Rate $ml\,an^{-1}hr^{-1}$	Grazing Rate $\frac{C\ grazed}{C\ part\text{-}algal}$ % day^{-1} Daytime	% Primary Prod. Grazed $\frac{C\ grazed}{C\ fixed}$ %	Filtering Rate $ml\,an^{-1}hr^{-1}$	Grazing Rate $\frac{C\ grazed}{C\ part\text{-}algal}$ % day^{-1} Nighttime	% Primary Prod. Grazed $\frac{C\ grazed}{C\ fixed}$ %
Cladocera						
Eubosmina coregoni						
Bosmina longirostris						
Daphnia retrocurva						
Daphnia galeata (A)						
Daphnia galeata (J)						
Holopedium gibberum (A)						
Holopedium gibberum (J)						
Polyphemus pediculus						
Leptodora kindtii						
Chydorus sphaericus				.215*	$.02\times10^{-4}$	.0009
Ceriodaphnia spp.						
Daphnia longiremis						
Copepoda						
Nauplii	.021±.011	2.81×10^{-4}	.1306	.048±.022	6.42	.2967
Diaptomus (A)	.166±.030	2.71	.1254	.100±.019	1.63	.0753
Diaptomus (C)	.088±.027	.31	.0141	.099±.024	.34	.0161
Cyclops bicuspidatus (A)	.098±.013	.26	.0120	.059±.013	.15	.0072
Cyclops bicuspidatus (C)	.099±.022	.34	.0155	.103±.014	.34	.0161
Tropocyclops prasinus						
Limnocalanus macrurus	.552±.274	.12	.0057	.494±.142	.11	.0055
Cyclops vernalis	-	-	-	.288±.104	.02	.0012
Mesocyclops edax	-	-	-	.893±.608	.08	.0040
Epischura lacustris						
Eurytemora affinis						
TOTAL	.142	6.55×10^{-4} hr^{-1} or 1.57%d^{-1}	.3033 or 30.3%	.171	9.11×10^{-4} hr^{-1} or 2.18%d^{-1}	.4230 or 42.3%

TABLE 13. GRAZING BUDGET ON NANNOPLANKTON, 28 MAY-2 JUNE 1975

Species	Filtering Rate mlan^{-1}hr^{-1}	Grazing Rate $\frac{\text{C grazed}}{\text{C part-algal}}$ % day^{-1}	% Primary Prod. Grazed $\frac{\text{C grazed}}{\text{C fixed}}$ %	Filtering Rate mlan^{-1}hr^{-1}	Grazing Rate $\frac{\text{C grazed}}{\text{C part-algal}}$ % day^{-1}	% Primary Prod. Grazed $\frac{\text{C grazed}}{\text{C fixed}}$ %
		Daytime			Nighttime	
Cladocera						
Eubosmina coregoni	.198±.023	89.32x10^{-4}	2.864	.198±.023	16.4x10^{-4}	.5261
Bosmina longirostris	.243±.025	60.22	1.932	.243±.025	8.78	.2817
Daphnia retrocurva				.455±.121	.80	.0257
Daphnia galeata (A)						
Daphnia galeata (J)						
Holopedium gibberum (A)						
Holopedium gibberum (J)						
Polyphemus pediculus						
Leptodora kindtii						
Chydorus sphaericus	—	—	—	.343±.106	1.36	.0436
Ceriodaphnia spp.						
Daphnia longiremis						
Copepoda						
Nauplii						
Diaptomus (A)	.134±.076	1.67	.053	.365±.052	2.09	.0670
Diaptomus (C)	.033*	.96	.031	.115±.023	1.66	.0532
Cyclops bicuspidatus (A)	.123±.053	.32	.010	.161±.042	1.98	.0637
Cyclops bicuspidatus (C)	.049*	7.48	.239	.168±.019	21.84	.7006
Tropocyclops prasinus						
Limnocalanus macrurus				.602*	.01	.0004
Cyclops vernalis						
Mesocyclops edax						
Epischura lacustris						
Eurytemora affinis						
TOTAL	.160	1.59.97x10^{-4} hr^{-1} or 38.39%d^{-1}	5.129 or 512.9%	.276	54.9x10^{-4} hr^{-1} or 13.2%d^{-1}	1.762 or 176.2%

TABLE 14. GRAZING BUDGET ON NETPLANKTON, 28 MAY-2 JUNE 1975

Species	Filtering Rate $\text{mlan}^{-1}\text{hr}^{-1}$	Grazing Rate $\frac{C \text{ grazed}}{C \text{ part-algal}}$ % day^{-1} Daytime	% Primary Prod. Grazed $\frac{C \text{ grazed}}{C \text{ fixed}}$ %	Filtering Rate $\text{mlan}^{-1}\text{hr}^{-1}$	Grazing Rate $\frac{C \text{ grazed}}{C \text{ part-algal}}$ % day^{-1} Nighttime	% Primary Prod. Grazed $\frac{C \text{ grazed}}{C \text{ fixed}}$ %
Cladocera						
Eubosmina coregoni						
Bosmina longirostris	.170*	4.20x10^{-4}	.1728	.045±.012	1.62x10^{-4}	.0667
Daphnia retrocurva				.037±.010	3.06	.1257
Daphnia galeata (A)				.140±.029	.24	.0102
Daphnia galeata (J)						
Holopedium gibberum (A)						
Holopedium gibberum (J)						
Polyphemus pediculus						
Leptodora kindtii				.056±.016	.22	.0091
Chydorus sphaericus						
Ceriodaphnia spp.						
Daphnia longiremis						
Copepoda						
Nauplii				.047*	17.44	.7162
Diaptomus (A)	.042*	.52	.0214	.075±.031	.43	.0177
Diaptomus (C)				.035±.012	.50	.0206
Cyclops bicuspidatus (A)	.104±.041	2.12	.0871	.088±.020	1.08	.0444
Cyclops bicuspidatus (C)				.053±.016	6.88	.2829
Tropocyclops prasinus						
Limnocalanus macrurus				.234*	.005	.0002
Cyclops vernalis						
Mesocyclops edax						
Epischura lacustris						
Eurytemora affinis						
TOTAL	.105	6.84x10^{-4} hr^{-1} or 1.63%d^{-1}	.2813 or 28.13%	.068	31.4x10^{-4} hr^{-1} or 7.55%d^{-1}	1.2937 or 129.37%

TABLE 15. GRAZING BUDGET ON NANNOPLANKTON, 5 AUGUST 1975

Species	Filtering Rate mlan^{-1}hr^{-1}	Grazing Rate $\frac{C\ grazed}{C\ part\text{-}algal}$ % day^{-1} Daytime	% Primary Prod. Grazed $\frac{C\ grazed}{C\ fixed}$ %	Filtering Rate mlan^{-1}hr^{-1}	Grazing Rate $\frac{C\ grazed}{C\ part\text{-}algal}$ % day^{-1} Nighttime	% Primary Prod. Grazed $\frac{C\ grazed}{C\ fixed}$ %
Cladocera						
Eubosmina coregoni	.011 ±.003	7.74x10^{-4}	1.3289x10^{-2}	.038 ±.007	26.74x10^{-4}	4.591
Bosmina longirostris	.009 ±.004	.8614	.1478	.034 ±.005	3.25	.559
Daphnia retrocurva	.032 ±.006	3.0649	.5260	.069 ±.017	29.01	4.980
Daphnia galeata (A)	.060*	1.3614	.2336	.095 ±.038	.035	.369
Daphnia galeata (J)				.060 ±.024	.022	.234
Holopedium gibberum (A)	.129 ±.044	9.2364	1.5853	.147 ±.042	10.523	1.806
Holopedium gibberum (J)	.050 ±.011	3.5795	.6140	.148 ±.026	10.595	1.818
Polyphemus pediculus	.044 ±.033	2.2170	.3800			
Leptodora kindtii				.034*	.308	.052
Chydorus sphaericus	.051 ±.035	5.3992	.9270	.038 ±.013	1.57	.270
Ceriodaphnia spp.				.270 ±.152	2.72	.467
Daphnia longiremis				.219 ±.038	1.10	.189
Copepoda						
Nauplii	.024*	7.8537	1.3480	.039 ±.036	12.76	2.190
Diaptomus (A)	.017 ±.004	.7539	.1290	.078 ±.014	3.46	.594
Diaptomus (C)	.007 ±.002	.8110	.1390	.054 ±.012	6.25	1.074
Cyclops bicuspidatus (A)	.011 ±.004	.4321	.0700	.043 ±.011	1.69	.290
Cyclops bicuspidatus (C)	.008 ±.002	1.7015	.2920	.033 ±.099	7.02	1.205
Tropocyclops prasinus	.008*	.0003	.0065	.043 ±.013	2.18	.374
Limnocalanus macrurus						
Cyclops vernalis	.015*	.1512	.0250	.073 ±.019	.02	.004
Mesocyclops edax	.088*	.4428	.0760	.058 ±.012	.04	.007
Epischura lacustris				.089 ±.042	.45	.077
Eurytemora affinis				.299 ±.026	.09	.015
TOTAL	.036	45.6085x10^{-4} hr^{-1} or 10.94%d^{-1}	7.822 or 782%	.078	119.833x10^{-4} hr^{-1} or 28.75%d^{-1}	21.165 or 2116%

TABLE 16. GRAZING BUDGET ON NETPLANKTON, 5 AUGUST 1975

Species	Filtering Rate mlan^{-1}hr^{-1}	Grazing Rate $\frac{\text{C grazed}}{\text{C part-algal}}$ % day^{-1}	% Primary Prod. Grazed $\frac{\text{C grazed}}{\text{C fixed}}$ %	Filtering Rate mlan^{-1}hr^{-1}	Grazing Rate $\frac{\text{C grazed}}{\text{C part-algal}}$ % day^{-1}	% Primary Prod. Grazed $\frac{\text{C grazed}}{\text{C fixed}}$ %
		Daytime			Nighttime	
Cladocera						
Eubosmina coregoni	.018±.005	12.66x10^{-4}	.152x10^{-2}	.006±.001	4.22x10^{-4}	.725
Bosmina longirostris	.007±.001	.66	.007	.005±.001	.41	.081
Daphnia retrocurva	.019±.003	7.98	.09	.014±.006	5.88	1.010
Daphnia galeata (A)	.030±.007	.67	.008	.020±.004	.45	.078
Daphnia galeata (J)	.013±.000	.28	.003	.018±.003	.41	.070
Holopedium gibberum (A)	.036±.006	2.57	.031	.037±.007	2.65	.454
Holopedium gibberum (J)	.025±.005	1.78	.021	.028±.003	2.00	.344
Polyphemus pediculus	.027±.011	.13	.001			
Leptodora kindtii	.054±.012	.48	.006	.034±.005	.31	.053
Chydorus sphaericus				.008±.001	.01	.001
Ceriodaphnia spp.	.008±.002	.32	.004	.021±.002	.87	.149
Daphnia longiremis				.025±.007	.01	.001
Copepoda						
Nauplii	.009*	.08	.000	.003*	.98	.168
Diaptomus (A)	.017±.004	.75	.009	.017±.004	.75	.130
Diaptomus (C)	.010±.001	1.16	.001	.006±.001	.69	.119
Cyclops bicuspidatus (A)	.010±.000	.39	.005	.008±.003	.31	.054
Cyclops bicuspidatus (C)	.009±.008	1.92	.002	.006±.002	1.28	.219
Tropocyclops prasinus	.008±.002	.37	.004	.017±.011	.80	.138
Limnocalanus macrurus						
Cyclops vernalis	.008±.001	.08	.000	.011±.003	.11	.019
Mesocyclops edax	.018±.011	.09	.001	.013±.002	.06	.011
Epischura lacustris	.031±.003	.16	.002	.016±.002	.08	.014
Eurytemora affinis				.026*	.01	.001
TOTAL	.019	32.5x10^{-4} hr^{-1} or 7.8%d^{-1}	.343x10^{-2} or .34%	.035	22.29x10^{-4} hr^{-1} or 5.35%d^{-1}	3.839 or 383.9%

TABLE 17. GRAZING BUDGET ON NANNOPLANKTON, 19 OCTOBER 1975

Species	Filtering Rate mlan^{-1}hr^{-1}	Grazing Rate $\frac{\text{C grazed}}{\text{C part-algal}}$ % day^{-1}	% Primary Prod. Grazed $\frac{\text{C grazed}}{\text{C fixed}}$ %	Filtering Rate mlan^{-1}hr^{-1}	Grazing Rate $\frac{\text{C grazed}}{\text{C part-algal}}$ % day^{-1}	% Primary Prod. Grazed $\frac{\text{C grazed}}{\text{C fixed}}$ %
		Daytime			Nighttime	
Cladocera						
Eubosmina coregoni	.016±.005	.295x10^{-4}	.003	.043±.029	.79x10^{-4}	.0094
Bosmina longirostris	.015±.010	.091	.001	.016±.005	.09	.0001
Daphnia retrocurva	.033±.008	.000	.000	.044±.041	.002	.0002
Daphnia galeata (A)	.034±.013	.001	.001	.067±.022	.130	.0016
Daphnia galeata (J)	.026±.006	.001	.001	.080±.026	.170	.0018
Holopedium gibberum (A)	.215±.084	.005	.003	.133±.032	.170	.0019
Holopedium gibberum (J)	.153±.063	.004	.002	.182±.087	.390	.0047
Polyphemus pediculus						
Leptodora kindtii						
Chydorus sphaericus						
Ceriodaphnia spp.						
Daphnia longiremis	.015*	.000	.000	.281*	.082	.0009
Copepoda						
Nauplii				.001*	.003	.0003
Diaptomus (A)	.004*	.000	.0000	.036±.007	.000	.0000
Diaptomus (C)	.039±.003	.014	.008	.020±.005	.007	.0420
Cyclops bicuspidatus (A)	.015±.003	.000	.000	.018±.010	.000	.0002
Cyclops bicuspidatus (C)	.008±.003	.011	.006	.016±.009	.982	.0116
Tropocyclops prasinus	.012±.004	.001	.001	.028±.019	.103	.0001
Limnocalanus macrurus						
Cyclops vernalis	.018±.004	.000	.000	.017±.018	.000	.0000
Mesocyclops edax						
Epischura lacustris	.032*	.000	.000	.037±.005	.000	.0000
Eurytemora affinis						
TOTAL	.050	.422x10^{-4} or .10%d^{-1}	.026 or 2.6%	.055	2.928x10^{-4} hr^{-1} or .70%d^{-1}	.0362 or 3.6%

fact, they grazed 70.7% of the standing crop (38.1% d^{-1} during daylight and 32.6% d^{-1} at night). When standing crops of phytoplankton are small, grazing 100% of daily productivity may be very significant.

The cruise of 12 April 1975 presented an opportunity to observe grazing at low temperatures (6.3°C). Copepods were the dominant herbivores (88% or 37342 of 42384 m^{-3}). Nauplii, while abundant, were characterized by a low filtering rate during daytime and grazed only 1.4% of the netplankton C fixed (Table 11). The copepodites of Diaptomus exhibited the highest filtering rates and grazed 12.1% of netplankton C fixed (7.8% during daytime and 4.3% at night). Cyclopoid copepodites were the second most important herbivore, consuming 11% of the netplankton C fixed (5.6% at night and 4.4% during the daytime). Thus, the crustacean community grazed 30.1% of the netplankton carbon fixed in April, and were characterized by a daytime grazing rate of 6.6% d^{-1} and a nighttime rate of 5.0% d^{-1}. In contrast, this same zooplankton community grazed 446% of the nannoplankton carbon fixed (Table 10), and had a daytime grazing rate (17.8% d^{-1}) about equal to the nighttime rate (18,5% d^{-1}) on nannoplankton. Obviously rates of carbon fixation for netplankton were low relative to the standing crop of netplankton carbon. The copepodites of Cyclops grazed 146% of nannoplankton production during the day and 109% during darkness (Table 10). Chydorus sphaericus grazed 28% and 50.8% of the primary production of small cells, whereas the copepodites of Diaptomus took 15.3% and 59.3% of the primary production during daylight and darkness. Obviously the nannoplankton was under heavy grazing pressure. This pressure was predominately from small grazers, chiefly copepodites of Cyclops and Diaptomus, and Chydorus sphaericus. The netplankton was not grazed to such an intense degree. These community foraging patterns thus characterize the classical synergistic effect of selective grazing, i.e., the enhancement of netplankton production by herbivores selectively grazing small cells (Tables 10-11).

One month later (5-9 May 1975) these same herbivores, including immature calanoids, were responsible for most grazing (Table 12). Nannoplankton was abundant (160.6 mg Cm^{-3}) but netplankton was not detected. The grazing rate on nannoplankton was greatly reduced; only 1.6% of the standing crop was grazed during daylight and 2.2% at night (Table 12). The percentage of nannoplankton carbon fixed which was grazed was significant (30.3% during daylight and 42.3% at night). Thus a total of 72.6% of the primary productivity of the previous day was removed by the herbivores; the standing crop could still double in 4 days. Most of the grazing was done by immature copepods; nauplii (13383 m^{-3}) and adult Diaptomus (1637 m^{-3}) accounted for most (88%) of the productivity removed.

By the end of May (28 May-2 June 1975), with warmer waters (14C), the grazing responsibility had shifted from the copepods to the cladocerans. Both the grazing rate and percentage of nannoplankton primary productivity grazed had increased (Table 13). The herbivores grazed 512.9% of the primary production during the day and 176.2% at night, for a total of 689.1%. The grazing rate or percentage of the standing crop grazed was also significant; 38.4% d^{-1} during daylight and 13.2 d^{-1} at night, or 51.6% d^{-1} of all available small phytoplankton. Eubosmina coregoni and Bosmina longirostris did most of the grazing (70.4% followed distantly by copepodites of Cyclops). Pressures on netplankton were much lower (Table 14).

Diversity of herbivores was greatest on 5 August 1975. Twelve species of cladocerans accounted for most (77%) of the grazing. The grazing rate on nannoplankton (relative volume water filtered or percentage of available food consumed) increased from the June level (Table 15). Of the available standing crop of nannoplankton, 10.9% d^{-1} and 28.8% d^{-1} were removed during daylight and darkness, for a total grazing rate of 39.7% d^{-1}. More significantly, 782% of the nannoplankton productivity was grazed during daylight, versus 2116% at night. Thus, on 5 August, when the netplankton was present in large quantities (74 mg Cm^{-3}), the grazing pressure upon nannoplankton was intense. We again emphasize that this selective pressure may have a synergistic effect in stimulating production of netplankton, since its presence as food is relatively low. In sharp contrast to the grazing upon nannoplankton, only 7.8 and 5.4% d^{-1} of netplankton standing crop was harvested (Table 16) for a total grazing rate of 13.2% d^{-1}. Only 0.34% and 383.9% of the netplankton carbon fixed was grazed (Grazing Impact) during day and night, respectively (Table 16).

By 19 October 1975, grazing as a control upon algal growth had become insignificant. The diversity of grazers remained high, but the mean community filtering rate on nannoplankton had dropped to 0.05 ml an^{-1} hr^{-1} (Table 17), from a high of 0.23 on 12 April (Table 10). Only Holopedium continued to filter at a high rate (0.21). Only 0.1% d^{-1} and 0.7% d^{-1} of the standing crop of nannoplankton was harvested during daytime and nighttime, respectively. In a similar respect, only 2.6% and 3.6% of the productivity of nannoplankton was grazed. In comparison, 0.1% and 0.7%, respectively, of the netplankton was grazed during daylight and darkness. Thus, in October 1975, with large populations of grazers, the nannoplankton had escaped from control by grazing. Obviously the late fall and winter period represent a time of low productivity and little zooplankton foraging. Nannoplankton populations have time to recover from intense summer grazing pressures, but under conditions of cold temperatures, reduced light, and slow growth rates.

Summary of Grazing by Taxonomic Grouping

The impact by order of the major crustacean grazers (Cladocera, Calanoida, and Cyclopoida) and unidentified immatures (nauplii) is most obvious if grazing by order is ranked for each of six intensive studies (Table 18). Considered are the percentage of nanno- and netplankton net productivity which was grazed each 24 hours. In addition, where one species or immature stage was dominant, its grazing impact is noted in parentheses.

During October 1974, total grazing on nannoplankton exceeded production, with 232% (158.4 + 73.7%) of the daily production grazed. The copepodites of calanoid copepods accounted for most of this; the major grazing on nannoplankton occurred during daylight hours. Netplankton production exceeded grazing. Approximately 95% of the netplankton productivity was grazed, again chiefly by calanoid copepodites.

Cyclopoid copepodites were dominant grazers in both April and May 1975. In April, cyclopoid copepodites grazed 255% of the nannoplankton productivity. A cladoceran, Chydorus sphaericus, was second in importance, removing 80%. Netplankton was lightly grazed in April, with only 28.7% removed, mostly by calanoid copepodites. Calanoid copepodites are typically larger than those of the cyclopoids and are possibly better at handling the larger netplankton. Little grazing occurred during May; the large netplankton diatoms were not present. Nauplii removed most (43%) of the 92% of the nannoplankton productivity grazed. Thus, during April and May, the grazing impact fell upon the nannoplankton, and small crustaceans (copepodites and nauplii) were implicated. Any grazing of netplankton which occurred (28.7% of productivity removed in April) was done by calanoid copepodites. Adult calanoids were not significantly involved.

During June and August 1975 (Table 18), the cladocerans were the important grazers. This was expected, since these crustaceans dominated or thrived during the warmer months. During June, Eubosmina coregoni, the larger of the two Bosmina species, took 339% of the nannoplankton productivity of the total of 629% grazed. Thus, the nannoplankton were again greatly overgrazed in June. In contrast, only 28.2% of the netplankton was controlled by the zooplankton. Most of the grazing on netplankton was done by cyclopoid copepodites and occurred during darkness.

Cladocerans removed 2107% of the total 2839% of nannoplankton productivity grazed during August 1975. Holopedium gibberum (520%) was especially important, grazing 362% of the previous day's productivity each night, as was Eubosmina coregoni (592%), which was also especially active at night (459%). Together Holopedium and Eubosmina combined to graze 152% of the netplank-

TABLE 18. PERCENTAGE OF NET PRIMARY PRODUCTIVITY GRAZED WITHIN SIZE GROUPS AND BY DAY AND NIGHT

Date	Rank, Order and Dominant Species		Daytime		Nighttime	
			Nanno	Net	Nanno	Net
October 1974	1.	Calanoida	94.1	31.4	39.3	32.5
		(Calanoid cops)	(61.3)	(13.1)	(22.6)	(32.0)
	2.	Cladocera	50.5	15.9	20.7	7.4
		(*Holopedium gibberum*)	(36.6)	(10.4)	-	-
	3.	Cyclopoida	13.8	4.9	13.7	2.9
		TOTALS	158.4	52.2	73.7	42.8
April 1975	1.	Cyclopoida	156.7	5.6	117.6	6.0
		(Cyclopoid cops)	(146.1)	-	(109.1)	-
	2.	Calanoida	32.8	9.3	59.8	5.1
		(Calanoid cops)	(15.3)	-	(59.3)	-
	3.	Cladocera	28.1	0.9	50.8	1.8
		(*Chydorus sphaericus*)	(28.1)	-	(50.8)	-
		TOTALS	217.6	15.8	228.2	12.9
5-9 May 1975	1.	Nauplii (mixed)	13.1	-	29.7	-
	2.	Cyclopoida	2.7	-	23.3	-
		(Cyclopoid cops)	-	-	(16.1)	-
	3.	Calanoida	13.9	-	9.1	-
	4.	Cladocera	-	-	-	-
		TOTALS	29.7	-	62.1	-
1 June 1975	1.	Cladocera	479.6	17.3	87.5	21.1
		Eubosmina coregoni	(286.4)	-	(52.6)	(12.5)
	2.	Cyclopoida	24.9	-	13.3	32.6
		Cyclopoid cops	(23.9)	-	-	(28.2)
	3.	Calanoida	8.4	-	15.0	3.7
		TOTALS	512.9	17.3	115.8	57.4
5 August 1975	1.	Cladocera	573.9	0.3	1533.5	296.6
		(Holopedium gibberum)	(158.5)	-	(362.)	(79.8)
		(Eubosmina coregoni)	(132.9)	-	(459.)	(72.5)
	2.	Cyclopoida	46.4	0	188.0	44.1
		(Cyclopoid cops)	(29.2)	0	(120.)	-
	3.	Mixed nauplii	84.8	0	219.0	16.8
	4.	Calanoida	26.8	0	166.8	26.4
		(Calanoid cops)	-	-	(107.4)	(11.9)
		TOTALS	731.9	0.3	2107.3	383.9
19 October 1975	1.	Cladocera	1.0	-	2.1	-
	2.	Cyclopoida	0.7	-	1.2	-
	3.	Calanoida	0.8	-	0.4	-
		TOTALS	2.5		3.7	
MEANS, ALL MONTHS	1.	Cladocera	188.9	5.7	282.4	54.4
	2.	Cyclopoida	40.9	1.8	59.5	14.3
	3.	Calanoida	29.5	6.8	48.4	11.3
		TOTAL OF MEANS	259.3	14.3	390.3	80.0

ton productivity. The cyclopoids (especially their copepodites), mixed nauplii, and calanoids were also important. August 1975 was characterized by large herbivorous zooplankton populations which removed more algae each day than was produced. Thus, standing crops were rapidly dropping in Lake Huron at that time, due chiefly to biological control.

By October 1975, only small populations of nannoplankton remained. These were little grazed (6.2% of productivity). The nannoplankton thus entered the winter months at very low population levels, due principally to the effect of the grazers earlier in the summer, but without grazing stress under winter conditions.

Mass Ingestion Rates

Mass ingestion rates provide an easily understood index to the grazing effectiveness of various herbivores, since they indicate the amount of algae ingested per unit body weight ($mgCd^{-1}$ mgC^{-1}). The decimal fraction is thus identical to the commonly expressed percentage of body weight per day (% wt. d^{-1}). For visual simplicity, the mass ingestion rates of cladocerans, calanoids, and cyclopoids have been coded with symbols as forms of circles, triangles, and squares, respectively (Figures 7-8). This coding enables the reader to discern the order whose members have normally high or low rates. The species codes are listed in Section 5.1.

Mass ingestion rates on nannoplankton (Table 19) in Southern Lake Huron were high from April through August, but fell abruptly in October. Typically, copepod nauplii and cladocerans were among the most efficient grazers on nannoplankton (Figure 7). In contrast, the adult calanoids were the least efficient, particularly copepodites and Diaptomus adults. At a maximum, nauplii ingested 0.54 mgC of algae per day per mgC of body tissue, or 5.4% of their weight. In August, in contrast, during October, nauplii ingested only .007% of their body weight in nannoplankton each day (Figure 7). One might presume that high mass ingestion rates on nannoplankton from May through August signified an abundant supply of food. Most likely during August and September 1975 this resource was overgrazed, leading to shortages in October. In October 1974, we had direct evidence for the overgrazing of nannoplankton.

If the nannoplankton are characteristic of oligotrophic lakes, it should be of interest to observe which species of zooplankton are most effective in cropping them. Previously it has been suggested that the calanoid copepods were the first herbivorous residents of the Great Lakes (McNaught, 1975). Thus, they should be good at grazing nannoplankton at low concentrations. But this does not imply that all stages consti-

TABLE 19. MASS INGESTION RATES ON NANNOPLANKTON (mgCd^{-1}mgC^{-1})

Species	Yearly Mean	Yearly Range
Fast Ingestors (Herbivores)		
Polyphemus pediculus	22.7x10^{-2}*	-
Mesocyclops edax (A)	12.8	4.6 - 2.09x10^{-2}
Nauplii (all copepods)	2.1	.007- 5.4
Chydorus sphaericus	2.1	0.33 - 3.2
Bosmina longirostris	1.6	0.04 - 3.7
Tropocyclops prasinus (A)	1.4	0.1 - 2.7
Cyclops bicuspidatus (A)	1.1	0.03 - 3.5
Daphnia galeata (A)	1.0	0.07 - 2.0
MEAN FAST ING.	5.6	
Slow Ingestors (Omnivores)		
Holopedium gibberum (A)	0.8x10^{-2}	0.1 - 1.4x10^{-2}
Cyclopoid copepodites	0.7	0.03 - 1.0
Eubosmina *coregoni*	0.6	0.06 - 0.98
Cyclops vernalis (A)	0.6	0.03 - 1.3
Limnocalanus macrurus (A)	0.5	-
Diaptomus spp. (A)	0.3	0.01 - 0.6
Holopedium gibberum (J)	0.3	0.2 - 0.5
Calanoid copepodites	0.2	0.03 - 0.5
MEAN SLOW ING.	0.5	
Non-ingestors (Predators)		
Leptodora kindtii	0.1x10^{-1}	

*22.7x10^{-2} mgCd^{-1}mgC^{-1} is equivalent to 22.7% of body weight d^{-1}.

tute the largest biomass, and we have seen that calanoid copepodites are the slowest of the slow ingestors (Figure 7). Calanoids are important with regard to total grazing in the lake (see Grazing by Taxonomic Grouping) simply because of their high numbers. It is the nauplii of both calanoid and cyclopoid copepods which are the most effective as well as the most common fast ingestors upon nannoplankton. The efficiency of this stage may reflect the evolution of the copepods in oligotrophic environments where nannoplankton predominates.

Great Lakes phytoplankton communities can be characterized by a predominance of small nannoplankton, which we have shown to be greatly overgrazed (Tables, 10, 12, 13, 15, 17). It is not surprising that the small specialized nauplii or earliest immatures of copepods, which evolved in oligotrophic Great Lakes, take large amounts of nannoplankton. What was surprising is that cladocerans like *Polyphemus*, *Chydorus*, *Bosmina longirostris*, and *Daphnia galeata* take 0.07 to 22.7% of their body weight in nannoplankton each day (Figure 7). Thus the warm water cladocerans, which have become a dominant fraction of Great Lakes communities in recent geological time, are the herbivores which overgraze the nannoplankton resource (see Grazing by Taxonomic Grouping), possibly synergizing, through concomitant excretion of algal nutrients, the production of netplankton.

In general, zooplankton crustaceans graze lightly upon the netplankton. Mass ingestion rates (yearly means) range from 0.1 to 1.3% of body weight per day (Figure 8). The mean yearly ingestion rate of 0.3% d^{-1} is only 10% of the mean yearly ingestion rate of netplankton (3.0% d^{-1}). Only *Chydorus* and *Tropocyclops* ingested significant amounts (Table 20). Indeed *Chydorus* may be a netplankton specialist, having been observed as a sessile sailor floating upon colonies of blue-green algae like *Gloeotrichia* (Birge, 1922). Most forms, including the abundant nauplii and copepodites, take less than 0.6% of their body weight in netplankton each day. The rare *Polyphemus*, long suspected of being a crustacean predator, but in reality an efficient specialist of nannoplankton, took almost no netplankton (0.1% wt. d^{-1}) (Figure 8).

Assimilation of Nannoplankton Foods

Nannoplankton (algae < 22 μm diameter) are clearly the food resource most heavily grazed by the crustacean zooplankton in Southern Lake Huron (Summary Table 18). These small algae are also readily digested and assimilated, as shown for the dominant members of the community on October, 1975 (Table 21). Eight species and two immature developmental stages (copepodites of calanoids and cyclopoids) were investigated. A sharp difference in relative assimilation of nannoplankton is noted. Most (6

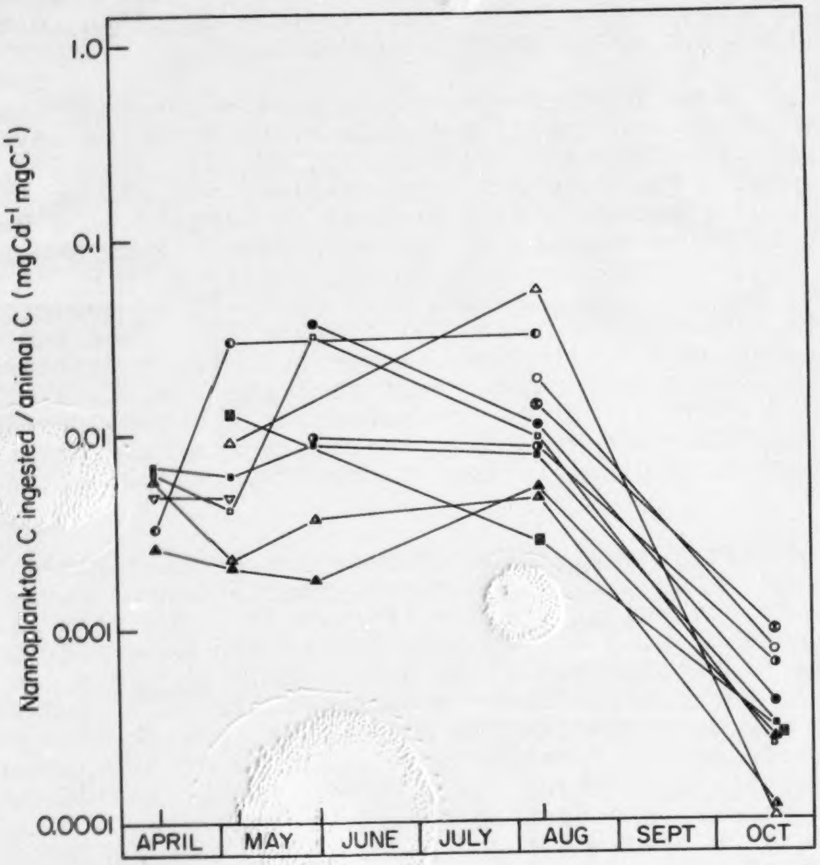

Figure 7. Mass ingestion rates (mgC plant day^{-1} mgC^{-1} animal) for dominant herbivores feeding on nannoplankton.

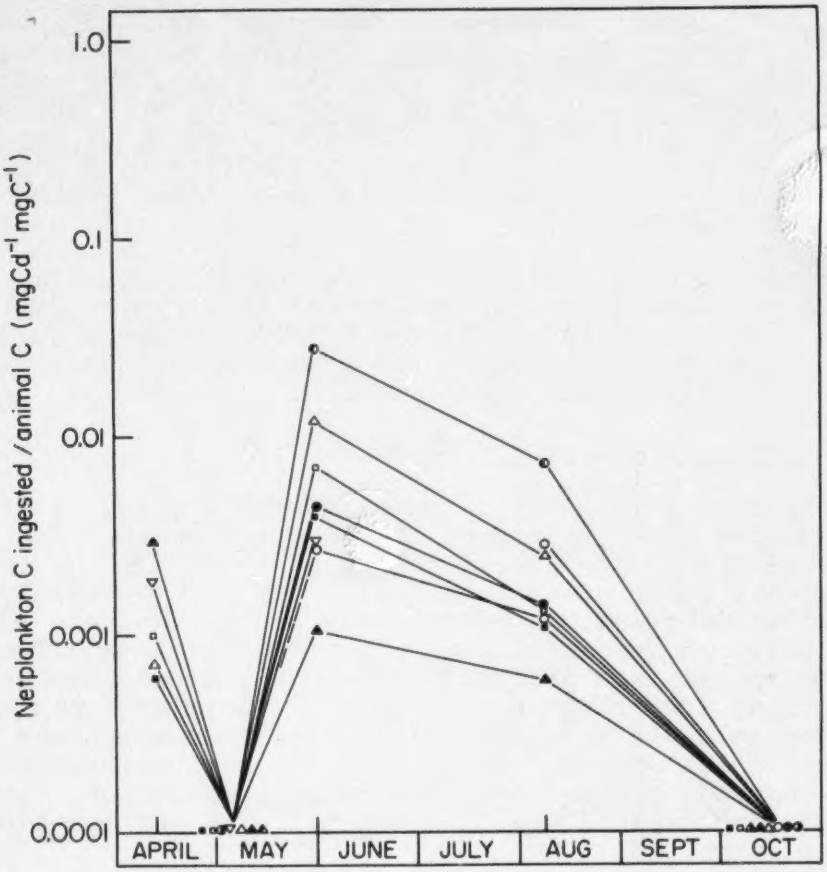

Figure 8. Mass ingestion rates (mgC $_{plant}$ day^{-1} mgC^{-1} $_{animal}$) for dominant herbivores feeding on netplankton.

species and cyclopoid cops) assimilated over 75% of algal carbon ingested (mean 93.2%, range 78.8 to 100%). These efficient assimilators were sharply divided from those crustaceans who ingested moderate amounts of nannoplankton (Tables 10, 12, 13, 15, 17) but assimilated less than 30% (mean 11.7%, range 0.5 to 26.3%).

High assimilators on nannoplankton included Diaptomus minutus, the important calanoid during October 1975, and the cyclopoids Cyclops bicuspidatus, cyclopoid copepodites, and Tropocyclops prasinus. Among the cladocerans, Eubosmina coregoni, Daphnia retrocurva, and Bosmina longirostris were characterized by high relative assimilation. On the other hand, Daphnia galeata and Holopedium gibberum were inefficient at assimilating nannoplankton, whereas the calanoid copepodites assimilated almost nothing (Table 21).

Clearly the majority of the crustacean community is well equipped to graze small nannoplankton. Filtration systems have evolved that are efficient in the removal of small cells. In a similar fashion, these herbivores have evolved enzyme systems that efficiently digest these foods.

Assimilation of Netplankton Foods

Netplankton (algae > 22 μm diameter) are assimilated to a lesser degree than the nannoplankton, just as they are less intensely grazed (Table 22). Again a clear difference is noted, with a small group of efficient assimilators (primarily copepodites) on netplankton, and a large group (adults of 8 species and nauplii) which assimilates significantly less. The netplankton specialists assimilated over 60% of algal carbon ingested (mean 74%, range 60 to 83.3%). Their most dominant members were calanoid and cyclopoid copepodites which are extremely abundant in Lake Huron. Thus, two principal categories of immature copepods are primary feeders on netplankton. Likewise, Eubosmina and Cyclops bicuspidatus had high assimilation efficiencies on netplankton.

More species had low assimilation efficiencies. Eight species of cladocerans and copepods, plus the very abundant copepod nauplii, assimilated less than 40% of the tagged foods ingested (mean 19.3%, range 3.4 to 37.5%). Nauplii assimilated only 18.2%; of all copepods, they are by far the most common plankters of Lake Huron. Thus, we see that copepods are not efficient at utilizing netplankton until they become copepodites and then lose this proclivity when they become adults (see Diaptomus, Epischura, Mesocyclops, Tropocyclops).

Biological Control Through Grazing

The control of populations of nuisance algae through en-

TABLE 20. MASS INGESTION RATES ON NETPLANKTON

Species	Yearly Mean	Yearly Range
Fast Ingestors (Herbivores)		
Chydorus sphaericus	1.3×10^{-2}*	$0.7 - 2.8\times10^{-2}$
Tropocyclops prasinus (A)	0.9	
MEAN FAST ING.	1.1	
Slow Ingestors (Omnivores)		
Nauplii (all copepods)	0.6	$0.7 - 1.5\times10^{-2}$
Cyclops bicuspidatus (A)	0.3	0.1 - 0.8
Daphnia galeata (A)	0.3	-
Bosmina longirostris	0.3	0.1 - 0.4
Mesocyclops edax (A)	0.3	-
Daphnia retrocurva	0.2	-
Cyclopoid copepodites	0.2	0.06- 0.4
Eubosmina coregoni	0.2	0.1 - 0.3
Cyclops vernalis (A)	0.2	-
Leptodora kindtii	0.2	-
Calanoid copepodites	0.2	0.06- 0.3
Limnocalanus macrurus	0.2	0.02- 0.3
Polyphemus pediculus	0.1	-
Diaptomus spp. (A)	0.1	0.06- 0.3
MEAN SLOW ING.	0.24	
MEAN ALL CRUSTACEANS	0.3	

*1.3×10^{-2} $mgCd^{-1}mgC^{-1}$ is equivalent to 1.3% of body weight d^{-1}.

TABLE 21. PERCENTAGE ASSIMILATION (mgC an^{-1} hr^{-1} assimilated/mgC an^{-1} hr^{-1} ingested) ON NANNOPLANKTON RESOURCES DURING OCTOBER 1975. ONE STANDARD ERROR IS INDICATED

High assimilators	Percentage assimilation
Diaptomus minutus	100 ± -
Cyclops bicuspidatus	100 ± 30
Cyclopoid copepodites	100 ± 12.6
Eubosmina coregoni	92.9 ± 14.2
Tropocyclops prasinus	92.0 ± 8.0
Daphnia retrocurva	88.9 ± 11.1
Bosmina longirostris	78.8 ± 13.5
MEAN	93.2
Low assimilators	
Daphnia galeata mendotae	26.3 ± 2.6
Holopedium gibberum (J)	11.0 ± 5.5
Holopedium gibberum (A)	9.1 ± 1.3
Calanoid copepodites	5.0 ± 0.0
MEAN	11.7

TABLE 22. PERCENTAGE ASSIMILATION (mgC an^{-1} hr^{-1} assimilated/mgC an^{-1} hr^{-1} ingested) ON NETPLANKTON RESOURCES DURING OCTOBER 1975. ONE STANDARD ERROR IS INDICATED

High assimilators	Percentage assimilation
Calanoid copepodites	83.3 ± 10.0
Eubosmina coregoni	80.0 ± 2.0
Cyclops bicuspidatus (A)	71.4 ± 10.0
Cyclopoid copepodites	60.0 ± 8.0
MEAN	73.6
Low assimilators	
Bosmina longirostris	37.5 ± 2.5
Cyclops vernalis	35.7 ± 2.9
Daphnia retrocurva	21.7 ± 4.3
Epischura lacustris	21.5
Tropocyclops prasinus	20.0 ± 2.0
Nauplii	
Diaptomus (A)	8.8
Holopedium gibberum (J)	7.0 ± 1.9
Mesocyclops edax	3.4 ± 0.3
MEAN	19.3

gineering methods (nutrient diversion) is expensive. One of the principal objectives of this study was to discover the degree of biological control in Southern Lake Huron exerted by each species of zooplankton. This was expressed as the species grazing impact (see Section 5.1, Eq. III), and was discussed extensively and summarized in Tables 10-17. If the species grazing impacts are summed for all species, we have the community grazing impact which can be expressed as either the percentage of nanno- or netplankton primary productivity ($mgCm^{-3}\ d^{-1}$) grazed by the zooplankton ($mgCm^{-3}\ d^{-1}$).

$$\text{IV) Community Grazing Impact} = \Sigma \text{ Species G.I.} = \frac{\Sigma \text{ algal carbon grazed}}{\Sigma \text{ algal carbon fixed}}$$

For each cruise on which selective grazing was determined, we synthesized as part of the analyses an estimate of community Grazing Impact (G.I.). These community G.I. for the period October 1974-October 1975 are presented in Figure 9.

Nannoplankton and netplankton populations in Southern Lake Huron were under the control of grazers from mid-May through mid-October (Figure 9). Unfortunately, limnologists do not have ready access to Southern Lake Huron during February and March when phytoplankton populations are beginning to grow more rapidly, leading to the pulse of diatoms in the spring. In April 1975, the phytoplankton community was dominated by the large diatoms *Tabellaria fenestrata*, *Fragilaria crotonensis*, and *Synedra filiformis*, and the nannoplanktons *Cryptomonas ovata* and *Rhodomonas minuta* (pers. comm., E. Stoermer). These large netplankton diatoms are not readily grazed, and the community grazing impact (C.G.I.) was 0.3 for netplankton. In early May, neither the nannoplankton (0.2) nor the netplankton (1.0) were growing much more rapidly than they were grazed. There was essentially an equilibrium between productivity and grazing (Figure 9). From early June through early August, the phytoplankton community was under the control of the grazers. The C.G.I. ranged from 6.2 to 25.3 for nannoplankton, reflecting the extreme grazing pressures and tight control over the growth of these small algae. Likewise, but to a much lesser degree, the sometimes noxious netplankton were under control during this time, with the C.G.I. ranging from 1.5 to 3.4 (Figure 9). Thus, the phytoplankton communities of Lake Huron are under the control of grazers throughout the growing season. This apparently healthy state must be maintained.

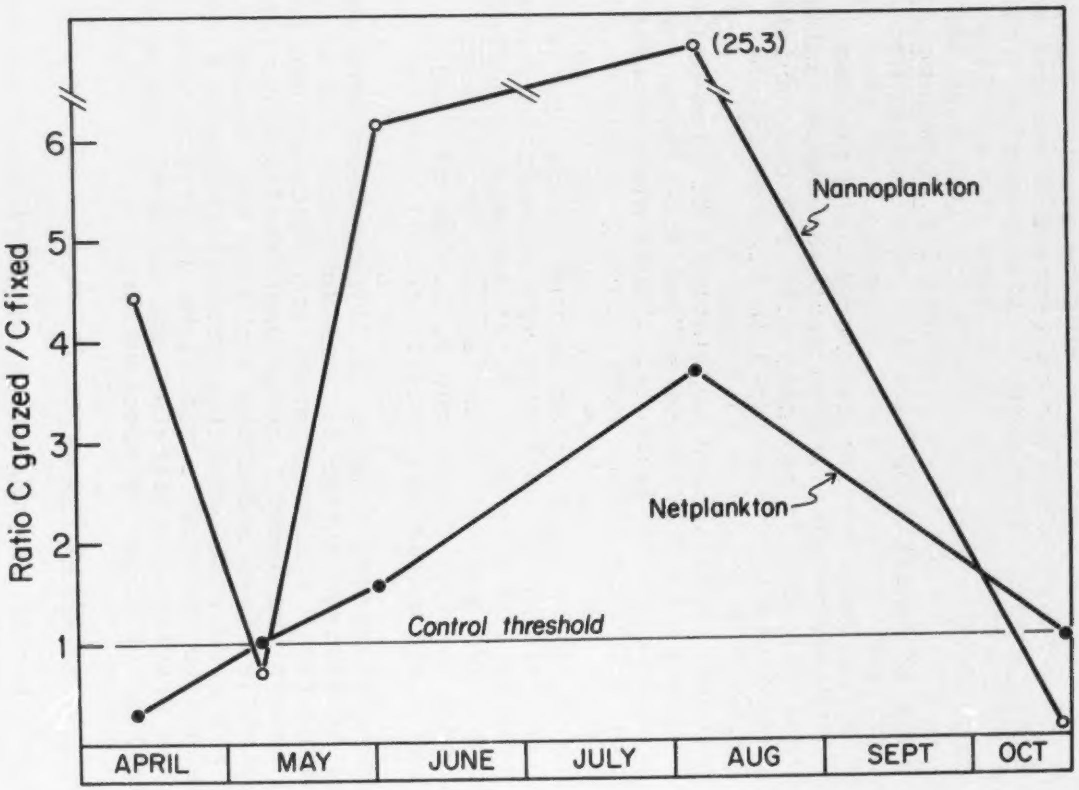

Figure 9. Control of phytoplankton by herbivorous zooplankton; ratio plant carbon grazed to carbon fixed.

5.3 EXPERIMENTAL MANIPULATION OF FOOD CHARACTERISTICS

Hypothesis and Significance

Copepods and cladocerans found in Southern Lake Huron have evolved in freshwater environments for over 12,000 years. The early day Laurentian Great Lakes were extremely oligotrophic, with phytoplankton populations dominated by small centric diatoms like *Cyclotella*, still prevalent in Lake Superior (Schelske *et al*., 1972). Calanoid copepods, which were the earliest inhabitants of these environments, may have fed upon such small diatoms, although both their feeding habits and food populations have evolved since (McNaught, 1975). Thus, the likelihood of size-selective grazing by extant forms is great. In more recent times, especially the last 40 years (McNaught and Buzzard, 1973), the cladocerans, which are typically warm-water inhabitants, have become abundant in the shoreward regions of Lake Huron and may constitute up to 85% of inshore populations. We have pictured them as generalists with regard to diet (they eat more blue-greens) and particularly with regard to size-selective feeding (they consume a broader range of sizes). Thus, the cladocerans are marked generalists, especially when contrasted with the highly specialized calanoids.

The purpose of these experiments was to define the mechanisms of selective feeding. Most likely the underlying factors are both quantifiable and interrelated. Size-selective feeding alone is too simple an explanation to explain the niche structure of the pelagic zooplankton; taste and shape of foods and other factors must be considered.

Understanding selective feeding is important in describing the behavior of herbivores at the organismic level, but is imperative to define their combined impact on phytoplankton populations at the ecosystems level. Selective feeding also implies that certain potential food resources are ignored. Underutilized foods may grow unchecked into noxious nuisance blooms. Such systems selection on algal populations is likely based both on selective grazing (inhibition) and nutrient remineralization (stimulation) of algae by zooplankton.

Selective Cropping of Paired Resources

Zooplankton graze at varying rates on different food resources. The initial analysis of these experiments consisted of calculating zooplankton filtering rates (ml $an^{-1}hr^{-1}$) upon paired algal resources, wherein one of the 6 pairs was a sheathed blue-green and the other an unsheathed green. The sheathed blue-greens *Anacystis nidulans* and *Gloeocapsa sp*. were paired with the unsheathed greens *Scenedesmus quadricauda*, *Ankistrodesmus falcatus*, and *Pediastrum sp*. Since the experiments were done in replicate, the results were amenable to an unpaired t-test; some samples yielded more subreplicates than others. Results showed whether zooplankton filtering rates were significantly higher on one algal species than another. However, these results did not indicate whether one food was selected or another rejected. This second analysis was accomplished using an electivity index. Those decisive characteristics (size and sheath) were further examined with a 2x2 factorial.

Most crustacean zooplankters were not highly selective feeders when presented with paired resources made up of 5 common algae. This generalization is based on the lack of selection of food by 5 dominant species (adult stage) and 2 immature stages (nauplii and cyclopoid copepodites) common enough to analyze without low numbers a priori indicating insignificance. Three common adult cyclopoids (*Cyclops bicuspidatus*, *C. vernalis*, and *Tropocyclops prasinus*) were not selective upon any of the 6 paired foods (Table 23). Likewise, the early immature copepod nauplii and the cladoceran, *Eubosmina coregoni*, were not selective. Thus, the predominant conclusion is that food selectivity is not a characteristic of these important herbivores; they took both sheathed and unsheathed blue-greens and greens of a variety of sizes. However, two dominant forms (adult *Diaptomus sicilis* and cyclopoid copepodites) were highly selective and deserve further analysis.

First we will analyze the original filtering rates of *Diaptomus* and the cyclopoid copepodites, since each showed different ingestion of the paired resources. *Diaptomus* selected the small sheathed *Gloeocapsa* over the large plain *Pediastrum*, (Table 23) with respective filtering rates of 0.087 vs. 0.043 ml an^{-1}hr^{-1}. Similiarly, the cyclopoid copepodites selected *Gloeocapsa* over *Scenedesmus* (filtering rates of 0.057 vs. 0.010 ml an^{-1}hr^{-1}. Thus, the small sheathed blue-green was always selected. In contrast, the greens were always selected when paired with the large sheathed blue-green *Anacystis*. *Diaptomus* selected the spined *Scenedesmus* over *Anacystis* (filtering rates of 0.021 vs. 0.009 ml an^{-1}hr^{-1}) as well as *Pediastrum* (filtering rates of 0.092 vs. 0.015 ml an^{-1}hr^{-1}). Thus, the large sheathed *Anacystis* was never selected. Now we can determine whether these different ingestion rates were due to active selection or simply the ignorance of specific foods.

Electivity Matrix of Resource Characteristics

For a better understanding of the functioning and later modeling of an ecosystem, it is desirable to identify those resource characteristics selected by herbivorous zooplankton. Electivities upon the 5 phytoplankton species presented in 6 pairs showed generally a selection for green algae when paired

TABLE 23. VARIATIONS IN FILTERING RATE ON GREEN(G) VERSUS BLUE-GREEN (BG) ALGAE BY COMMON HERBIVORES OF LAKE HURON. SIGNIFICANTLY ($**\alpha = .01$; $*\alpha = .05$; NS = NOT SIGNIFICANT) HIGHER FILTERING RATES ON ONE MEMBER OF PAIR INDICATED: (-) INDICATES LACK OF SIGNIFICANT NUMBERS OF TRIALS

	Small sheathed bluegreen Gloeocapsa paired with		
Herbivore	Scenedesmus	Ankistrodesmus	Pediastrum
Diaptomus sicilis(A)	NS	NS	BG*
Cyclops bicuspidatus(A)	NS	NS	NS
Cyclops vernalis(A)	NS	NS	NS
Tropocyclops prasinus(A)	NS	-	NS
Cyclopoid copepodites	BG*	NS	BG*
Copepod nauplii	NS	NS	NS
Eubosmina coregoni(A)	NS	-	NS
	Large sheathed bluegreen Anacystis paired with		
	Scenedesmus	Ankistrodesmus	Pediastrum
Diaptomus sicilis(A)	G**	NS	G*
Cyclops bicuspidatus(A)	NS	NS	NS
Cyclops vernalis(A)	-	-	-
Tropocyclops prasinus(A)	NS	NS	NS
Cyclopoid copepodites	NS	NS	G*
Copepod nauplii	NS	NS	NS
Eubosmina coregoni(A)	-	-	-

with a large blue-green and for a very small blue-green when paired with a variety of greens (Table 23). Thus, neither the greens nor the blue-greens were selected consistently, nor were the smaller species always preferred. Since the five resources had other characteristics than just taxon and size, such properties deserve further attention.

Both blue-greens (*Gloeocapsa* and *Anacystis*) have a sheath or gelatinous matrix. The species of *Scenedesmus* (*quadricauda*) was selected for its unusually long spines. *Ankistrodesmus*, usually found in fasicles of long crescent-shaped cells, was considered unspined and clearly unsheathed. *Pediastrum*, a large colony of cells, was considered to have such short lobes that it was emarginate or unspined. Thus, experimentally determined electivities upon these various resources can be placed in a matrix where size (large vs. small) can be paired with the presence of spines or the presence or absence of a sheath (Table 24). Ivlev's (1955) electivity index(E) was employed, where:

$E = (R-P)/(R+P)$ and wherein

R = proportion of resources taken

P = proportion of total resources available

The resource characteristics matrix (Tables 24-25a) is useful in determining the degree to which size, sheath, or spines influence electivity. By summing the rows we obtain the mean electivity by size, and by summing the columns, the electivity for spined and sheathed cells. These electivities were then ranked (Tables 24-25b). *Diaptomus sicilis*, a large omnivorous calanoid copepod, selected large plain green algae (*Pediastrum*) in proportions greater than offered ($E = 0.20$). *D. sicilis* took small *Ankistrodesmus* and the small sheathed blue-green (*Gloeocapsa*) in nearly equivalent numbers to those present ($E = -0.006$ and -0.05). This numerous large herbivore rejected small spined greens (*Scenedesmus*, $E = -0.2$) and large sheathed blue-greens (*Anacystis*, $E = -0.4$). Selection ($E > 0$) can be differentiated from ingestion of what is available ($E = 0$) and ignorance or lack of utilization ($E < 0$). But the difference between ignoring and actively rejecting a resource is not evident. Clearly *Diaptomus* (adults) reacted to food size as well as the presence or absence of sheaths and spines in feeding selectively.

The resource characteristics matrix (Table 25a) for [redacted]lar to that for *Diaptomus*. The highest electivity occurred when a large plain cell (*Pediastrum*) was offered with a small sheathed cell (*Gloeocapsa*). In ranked order of preference, these numerous immature copepods selected

TABLE 24. a) MATRIX OF RESOURCE CHARACTERISTICS AND b) RANKED FOOD CHARACTER PREFERENCES FOR *Diaptomus sicilis* (E = ELECTIVITY)

a)

		spined	sheathed		
		small	large	small	
Unspined and Unsheathed	small	-.20 -.02	-.18 -.04	-.02 +.04	E = -.006 small plain
	large	-.20 -.07	-.62 +.20	-.07 +.48	E = .20 large plain
		E = -.20 small spined	E = -.40 large sheathed	E = -0.045 small sheathed	

b) Preference by Rank of Food Electivity

Characteristic	Order	E
large plain	G	+.20
small plain	G	-.006
small sheathed	BG	-.05
small spined	G	-.20
large sheathed	BG	-.40

TABLE 25. a) MATRIX OF RESOURCE CHARACTERISTICS AND b) RANKED FOOD CHARACTER PREFERENCES FOR CYCLOPOID COPEPODITES (E = ELECTIVITY)

a)

		spined	sheathed		
		small	large	small	
Unspined and Unsheathed	small	-.59 +.05	-.11 +.03	-.14 +.05	E = +.04 small plain
	large	-.10 +.05	-.21 .11	-.10 +.22	E = +.126 large plain
		E = -.32 small spined	E = -.16 large sheathed	E = -0.12 small sheathed	

b) Preference by Rank of Feed Electivity

Chracteristic	Order	E
large plain	G	+.126
small plain	G	+.04
small sheathed	BG	-.12
large sheathed	BG	-.16
small spined	G	-.32

large plain and small plain cells and ignored the spined and sheathed cells to differing degrees (Table 23b). Large sheathed cells were taken less frequently than small sheathed cells, and spined cells were taken the least. In fact, by number they constituted 50% of the food offered, but only 15.1% of the ingested amount when paired with Gloeocapsa. This analysis had one fault in that size and sheathness were not examined independently.

Effect of Sheath and Size Upon Ingestion

A 2x2 factorial (parametric) was employed to discover whether the effect of the sheath or relative size was independently the most important factor influencing selection of food. Filtering rates for Diaptomus and cyclopoid copepodites on paired resources, previously shown as being significantly different (Table 24), were cast into a 2x2 factorial to test the effect of size versus that of sheath. The presence or absence of a sheath was the overwhelming factor of importance determining whether a resource was ingested or ignored, both in the case of Diaptomus (***, $P < .001$) and cyclopoid copepodites (***, $P < .001$); it is noteworthy that the interaction was not significant (Table 26). Thus, in modeling food electivity, we can rank the sheath and associated ramifications of taste and inhibitory substances combined with it, above size as a matter of critical importance. Two herbivores which were highly selective ignored sheathed forms and selected large plain resources. From the opposing viewpoint of resource fitness, it is best to be large and sheathed, and this is precisely the direction in which blue-green algae which form blooms, like Anacystis, have evolved.

Utilization of Electivities in Modeling Grazing

Modelers should utilize electivities on specific phytoplankters in modeling zooplankton grazing. In addition to the filtration rates characterizing specific herbivores, electivity terms may be used to estimate selectivity on individual resources. Electivity by fishes on zooplankton was employed to estimate selective importance of size and simulate fish predation (McNaught and Scavia, 1976). These first estimates of electivity for zooplankton grazing on common phytoplankton should be immediately applicable to modeling grazing in Lake Huron and other unproductive lakes where these phytoplankters occur.

Purpose of Experiments with Beads

The size range of food particles and their selective harvest by herbivores remains of critical importance to understanding the eutrophication of aquatic ecosystems; lake aging is usually accompanied by successional changes in algal popula-

TABLE 26. TWO-LEVEL ANOVA WITH UNEQUAL SAMPLE SIZE SUMMARIZING EFFECTS OF SHEATH AND FOOD SIZE ON FILTERING RATES OF *Diaptomus* AND CYCLOPOID COPEPODITES. (α = .001 (***), α = .05 (*))

Diaptomus

Source of Variation	df	MS	F
Subgroups			
A(sheath)	1	.43	71.0***
B(food size)	1	.02	3.9
A x B (interaction)	1	.03	4.8*
Within Subgroups (error)	42	.006	
TOTAL	45		

Cyclopoid copepodites

Source of Variation	df	MS	F
Subgroups			
A(sheath)	1	.23	25.5***
B(food size)	1	.03	2.9
A X B (interaction)	1	.03	3.5
Within Subgroups (error)	29	.004	
TOTAL	32		

tions, with larger forms assuming dominance. Experimentally one can provide a uniform food source which varies only by size and not in shape or taste. Polystrene beads were selected because they are spherical in shape and uniform in chemical composition. Such beads were added in small numbers to natural populations of algae; the beads were of a known size-distribution and later were readily identified in the guts of preserved zooplankton (see Section 4.3, Methods).

Results of Size Selection Experiments with Beads

Copepod nauplii--

Copepod nauplii were the most abundant grazers in Southern Lake Huron. When presented with a natural population of phytoplankton spiked with beads, which were most numerous in abundance at a diameter of 3 μm (Figure 10, top), they selected beads approximately 1 μm in diameter (Figure 10, middle). These small beads were relatively rare in the bead population, as evidenced by an Ivlev electivity (E) of greater than 6 (Figure 10, bottom). Beads of a diameter of 2 μm were taken in equivalent numbers to those offered (E = 20). Thus, nauplii, the smallest of the herbivores, were highly size-selective feeders when presented a population of small, spherical, uniform beads which were rare in a zooplankton of natural phytoplankton. The beads were in effect a non-radioactive tag.

Copepod copepodites--

Copepod copepodites (DC) are the second most abundant group of grazers (Section 5.4; Appendix). When presented beads under the same experimental conditions as above, they selected beads of approximately 0.5 μm diameter (Figure 10, middle). Thus, the two most abundant herbivores in Southern Lake Huron are highly size-selective; the Ivlev electivity index for copepodites selecting such small 0.5 μm particles was 5.5 (Figure 10, bottom), but dropped to 0 for particles of 2 μm diameter, indicating no selection. Thus, copepodites relied upon food particles less than 2 μm diameter, most likely small algae and bacteria.

Diaptomus sicilis (adults)--

Adult calanoid copepods are most likely omnivorous, since they consume an average of 4% of their body weight per day (Section 5.1). It has been our hypothesis that adult calanoids are adapted to feeding on small phytoplankters characteristic of the waters in which they live. *D. sicilis* took beads very small (< 1 μ) which was surprising *given* its large size (1.2 to 1.9 mm), but certainly not its natural spectrum of small foods. Oligotrophic lakes commonly contain populations of nannoplankton less than 20 μm diameter (McNaught, 1975). The adults also feed on the peak frequency of food items (3 μm). This is evidence that "tracking" (Richman *et al*. 1977) of the predominant size

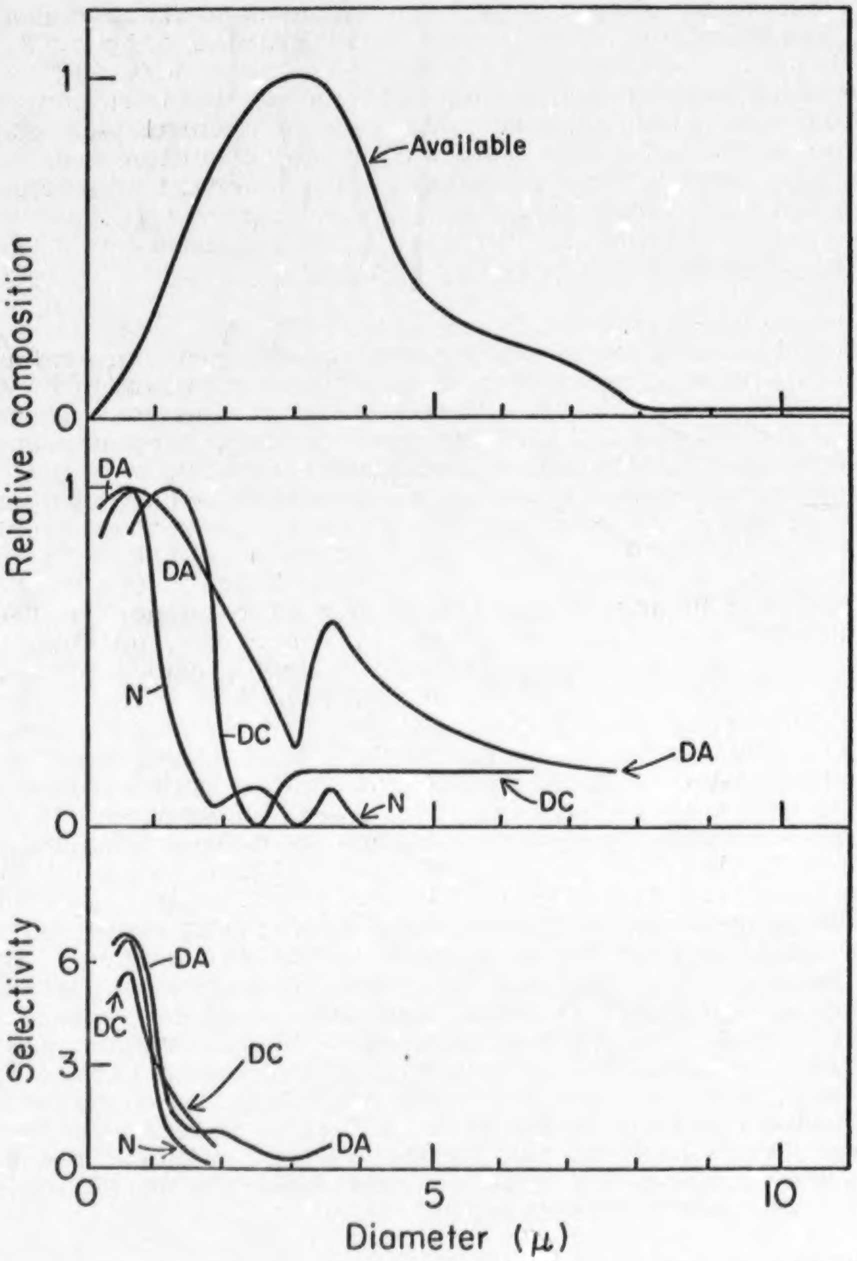

Figure 10. Selective ingestion of beads by Diaptomus sicilis adults (DA), copepodites (DC), and nauplii (N). Composition of gut (middle) relative to bead population available (upper); selectivity expressed as Ivlev's index (lower).

particle may have played a part in their feeding behavior (Figure 10, middle).

Cyclops bicuspidatus (adults)--
Adult cyclopoid copepods are also omnivorous and consume an average of 5% of their body weight per day (Section 5.1). When *Cyclops* adults were presented with a natural population of phytoplankton spiked with beads, they took the smallest beads of 0.5 μ diameter (Figure 11, middle), with maximum electivity (E = 1) at that diameter (Figure 11, bottom).

Thus, size selection for small foods (0-5 μm), in a food spectrum that is exceptionally broad (0-125 μm), was characteristic of these dominant herbivores in this oligotrophic ecosystem. This conclusion was reached using an experimental food (beads) which varied in size but not in shape or taste. These experiments were conducted in the field with animals acclimated to their natural measure of the size preference of these species and life stages.

5.4 HORIZONTAL DISTRIBUTIONS OF DOMINANT ORGANISMS

Description of Distribution of Dominant Species

Distributions of the dominant species of crustaceans are presented; since a large amount of distributional data has been collected and is available, only the distributions for the month of maximum abundance for each life stage or species has been presented. Detailed summaries are found in the Appendix (Section A).

In examining these distributions, the influences of the physical limnology of Southern Lake Huron are evident. First, surface waters enter Saginaw Bay from the northeast, circulate in a counter clockwise fashion, and spill out into the main lake around the thumb (Pointe aux Barques). This dominant pattern of circulation, in addition to the highly eutrophic nature of Saginaw Bay, influences all of our distributions. Secondly, the calanoids tend to be found in offshore waters, whereas the cladocerans grow best in the warmer inshore areas. These differences are evident and must be considered in utilizing these groups as pollution indicators.

Calanoid copepods--
The Calanoids are large, herbivorous or carnivorous copepods common to cold, well oxygenated, and generally oligotrophic waters. They commonly have been referred to as clean-water indicators. Usually the nauplii and copepodites are herbivorous (Section 5.1), while the adults become carnivorous. In the Great Lakes, the adult calanoids of the genus *Diaptomus* are

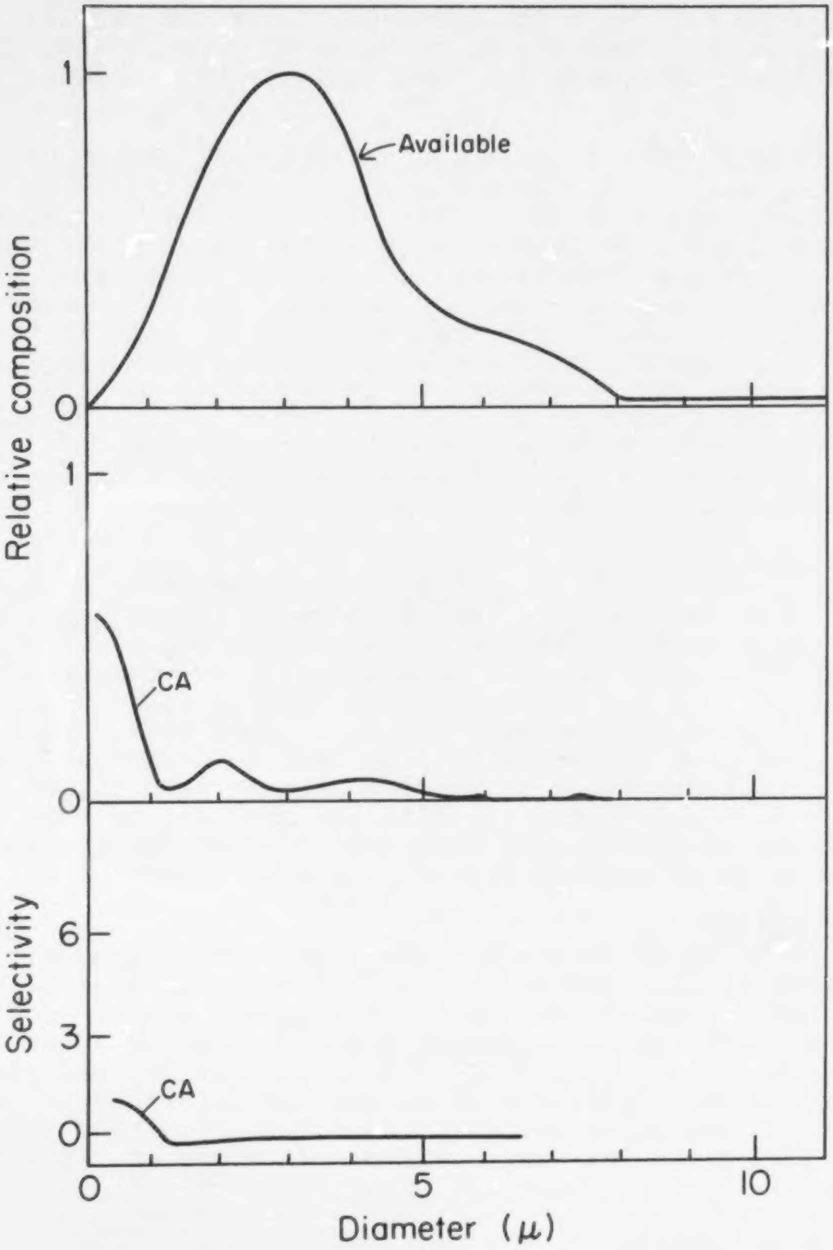

Figure 11. Selective ingestion of beads by Cyclops bicuspidatus (adults). For description see Fig. 10.

highly sensitive to predation. Thus, where predation, especially by the alewife Alosa pseudoharengus, is common, adult distributions must be carefully interpreted. Since the nauplii, and to some extent the copepodites, are free from predation, distributions of these immatures may best indicate high quality waters.

Nauplii--

These small (40 µm) immatures of both calanoid and cyclopoid copepods were most abundant in the surface waters (0 to 5 m) of the midlake region in June 1974. Here concentrations of 50,000 animals m^{-3} were common, with localized densities over 150,000 m^{-3} offshore from Goderich, Ontario (Figure 12). In contrast to the open-water nursery grounds, the outer waters of Saginaw Bay supported less than 40,000 m^{-3}. This is indicative of the low quality of these waters, especially since stations near Tawas, representative of the input of nauplii to Saginaw Bay, had densities of over 100,000 m^{-3}. It should be noted that the above discussion applies to the nauplii of all copepods. Nauplii are more abundant than copepodites and adults, since significant early season mortalities occur.

Calanoid copepodites--

Probably the best high quality environmental indicators, the copepodites of Diaptomus, and to a small extent, Epischura and Scenecella, provided insight because they require clean waters, yet are more likely to escape predation than their respective adults. Again inshore waters leaving Saginaw Bay contained less than 10,000 animals m^{-3} in October 1974. Whereas the open waters had concentrations as high as 64,800 m^{-3}, with most locations represented by numbers greater than 40,000 m^{-3} (Figure 13) during October. As with the nauplii, an area of low concentration was evident northeast of Port Huron, possibly due to upwelling of deep waters in this area (Stations 60, 65).

Diaptomus minutus--

Adults (♀ and ♂) were much less common than copepodites, yet exhibited similar patterns of distribution (Figure 14). Following the copepodite abundance in October, adults of D. minutus were most common in November 1974. Inshore areas were characterized by less than 2,000 m^{-3} in Saginaw Bay and along the Michigan coast. Offshore areas and the Ontario coast were represented by densities greater than 4,000 m^{-3}, while a pocket of maximum abundance was again evident off Goderich, Ontario (Station 58).

Diaptomus oregonensis--

Again adults (♀ and ♂) were most abundant during November 1974. Less than 750 m^{-3} were found in outer Saginaw Bay and along the Michigan coast. The Ontario shores were characterized by densities greater than 1,000 m^{-3}, while a pocket in Southern Lake Huron (Stations 60, 64, 66) had numbers above 1,500 m^{-3} (Figure 15).

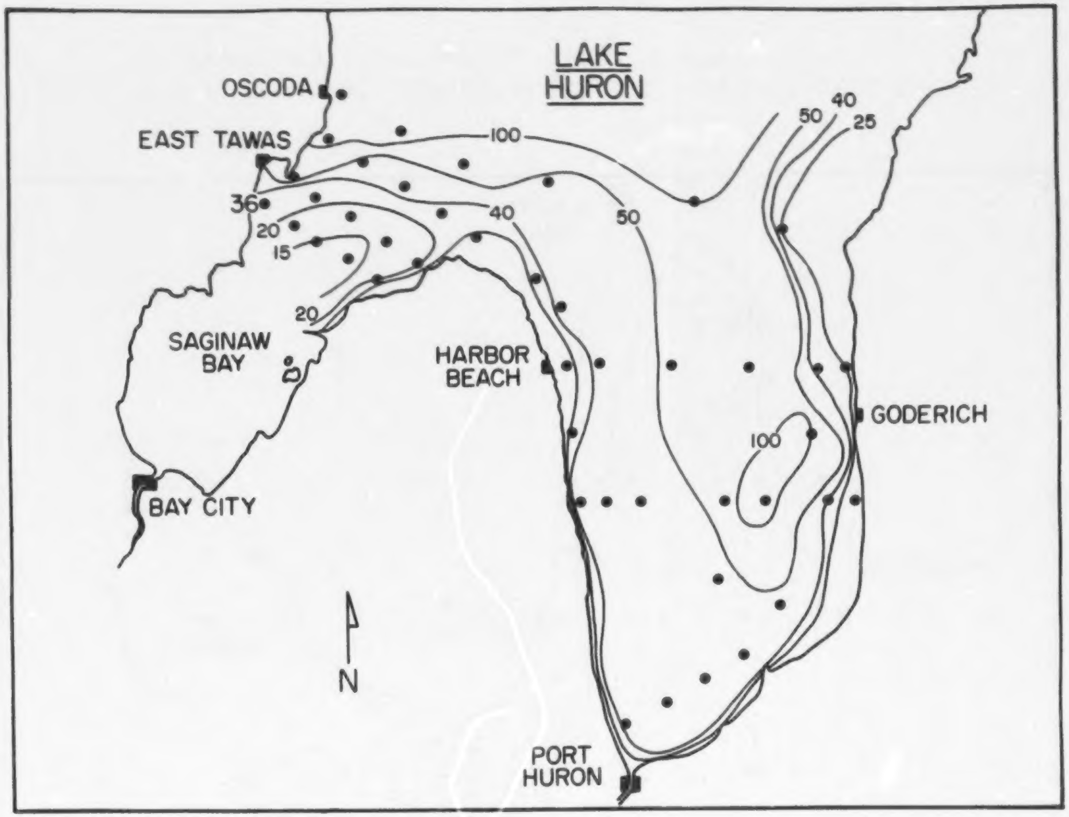
LAKE HURON
OSCODA
EAST TAWAS
SAGINAW BAY
BAY CITY
HARBOR BEACH
PORT HURON
GODERICH
N
100
50
40
36
20
15
20
50
40
25
100

Figure 12. Horizontal distribution of nauplii in Southern Lake Huron, 16-21 June 1974.

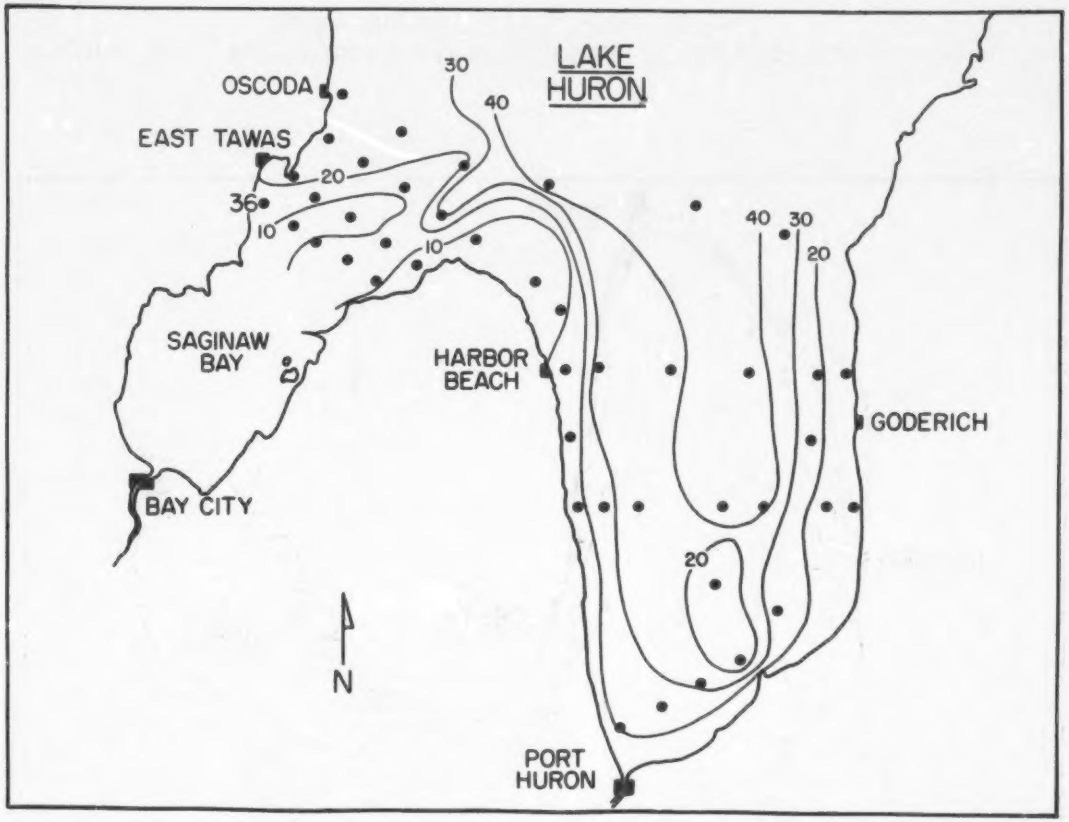
LAKE HURON
OSCODA
EAST TAWAS
SAGINAW BAY
BAY CITY
HARBOR BEACH
PORT HURON
GODERICH
N
30
40
20
36
10
10
40
30
20
20

Figure 13. Horizontal distribution of calanoid copepodites in Southern Lake Huron, 8-12 October 1974.

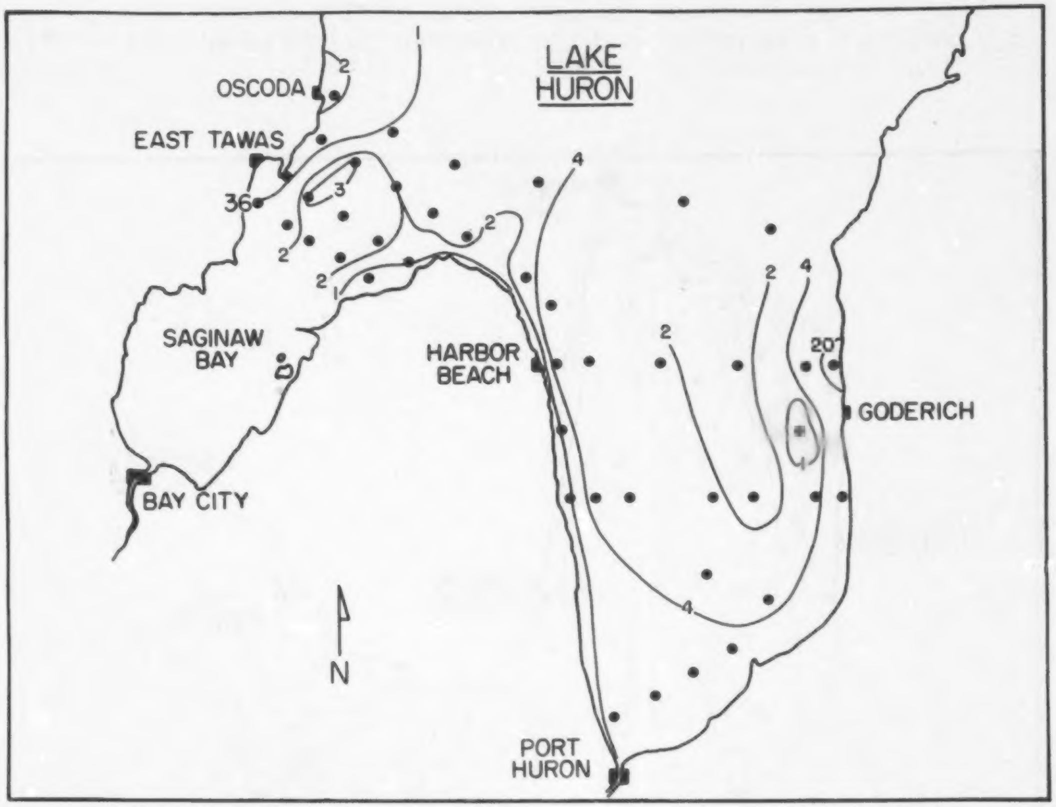
LAKE HURON
OSCODA
EAST TAWAS
36
SAGINAW BAY
BAY CITY
HARBOR BEACH
PORT HURON
GODERICH
N
1
2
3
4
20

Figure 14. Horizontal distribution of Diaptomus minutus in Southern Lake Huron, 10-14 November 1974.

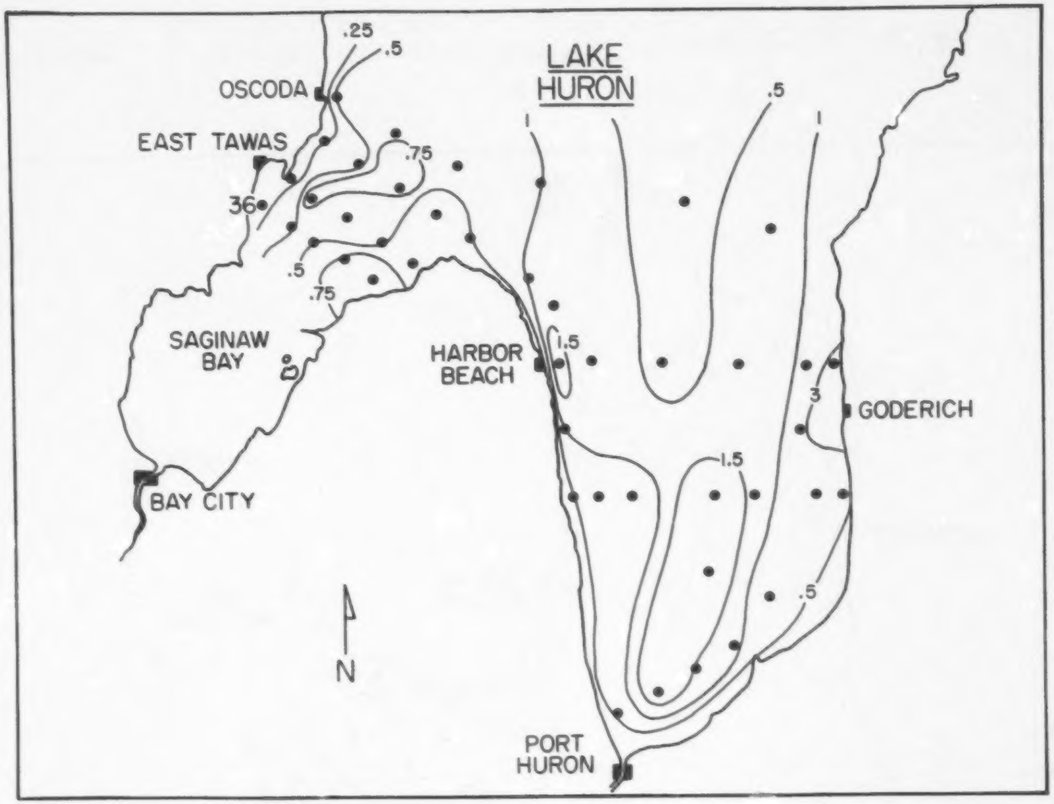
LAKE HURON
OSCODA
EAST TAWAS
SAGINAW BAY
BAY CITY
HARBOR BEACH
PORT HURON
GODERICH
N
.25
.5
.75
.5
.75
36
1
.5
1
1.5
3
1.5
.5

Figure 15. Horizontal distribution of Diaptomus oregonensis in Southern Lake Huron, 10-14 November 1974.

Diaptomus sicilis--

This organism is the original colonizer of the Great Lakes. Today, Diaptomus sicilis is the most important species in Lake Superior, and most likely represents our best oligotrophic indicator. In all areas, densities increased from shore toward open lake. Maximum numbers were found during November 1974 in the midlake region, with an additional small pocket off Goderich, Ontario (Figure 16). Frequent observation of high standing crops near Goderich (Station 58) may point to the unique nature of this area of the lake. Other investigators in the team have spoken of high nutrient concentrations in this area (Stoermer, 1978), which may be related to increased primary production.

Cyclopoid copepods--

The adult cyclopoids are predaceous and may reflect abundances of prey organisms (immature copepods and cladocerans) rather than clean waters. Thus, their distributions are presented with little or no inference at this time concerning their use in applied water quality work.

Cyclopoid copepodites--

In marked contrast to the calanoid copepodites, these immature cyclopoids were most common in inshore waters in November, 1974. Densities as high as 35,000 m^{-3} were found in outer Saginaw Bay, whereas the open water contained only 15-20,000 at most stations (Figure 17). Thus, high densities probably reflect the high quantity of available food resources in more eutrophic waters. In contrast to the calanoids, these copepodites are most abundant in the late fall.

Cyclops bicuspidatus--

As this is by far the dominant cyclopoid of Southern Lake Huron, most of the above copepodites developed into C. bicuspidatus. Yet with strong surface currents carrying copepodites out of Saginaw Bay, maximum densities (6,000 m^{-3}) of adults occurred in inshore waters of Saginaw Bay in June, 1974. The densities on the Tawas and Harbor Beach areas were similar, indicating that adults may enter and leave the Bay with little change in population size. A second pocket of abundance was evident in the midlake area (Figure 18) and again above Goderich.

Tropocyclops prasinus--

This relatively rare cyclopoid was common along the Michigan coast in the area of Harbor Beach (Figure 19).

Cladocera--

All cladocerans appear to prefer warm, inshore waters. They are generally characterized by high birth rates. These high natal rates are maintained by heavy grazing on phytoplankton which is characterized by high mass ingestion rates (Section 5.1). Thus, distributions of the cladocera are vital to understanding Southern Lake Huron. They reflect, among other eco-

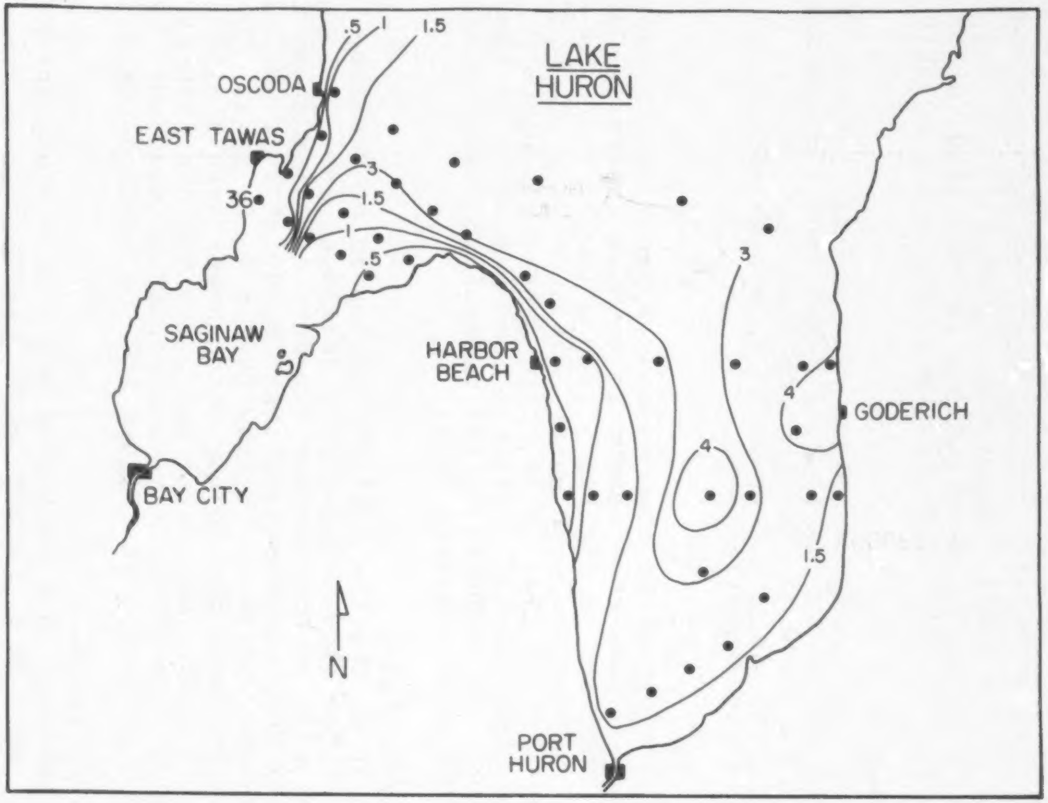
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Figure 16. Horizontal distribution of Diaptomus sicilis in Southern Lake Huron, 10-14 November 1974.

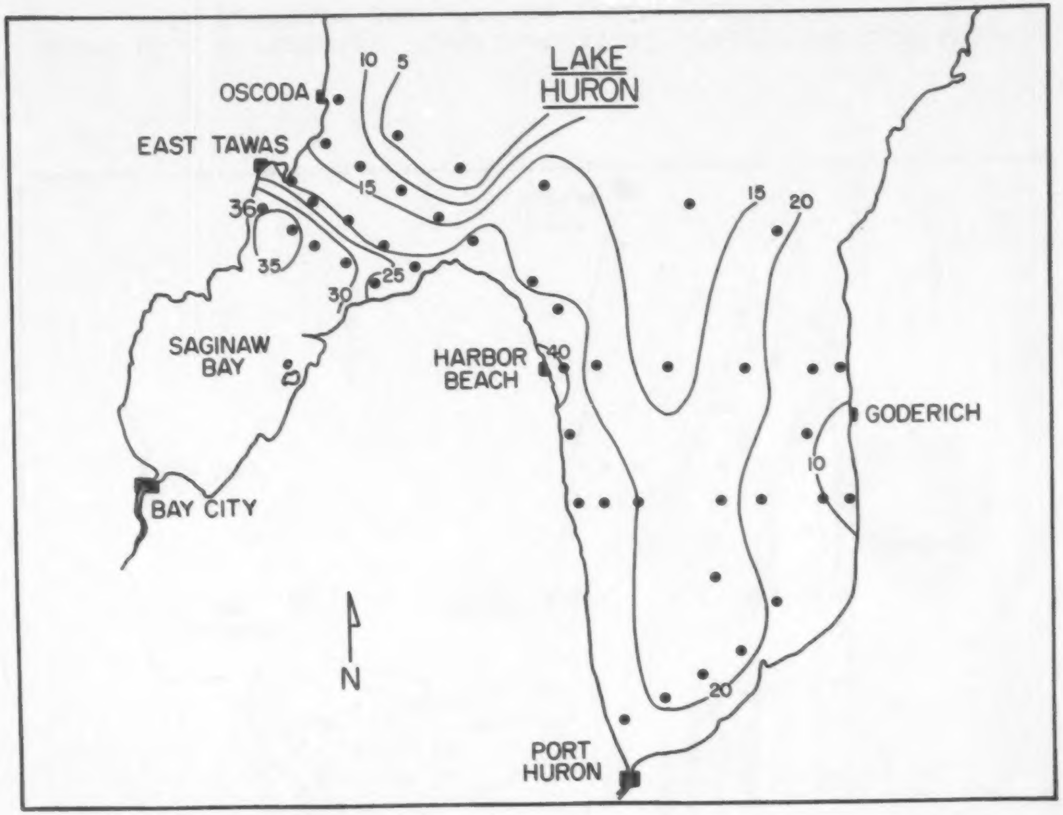
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Figure 17. Horizontal distribution of cyclopoid copepodites in Southern Lake Huron, 10-14 November 1974.

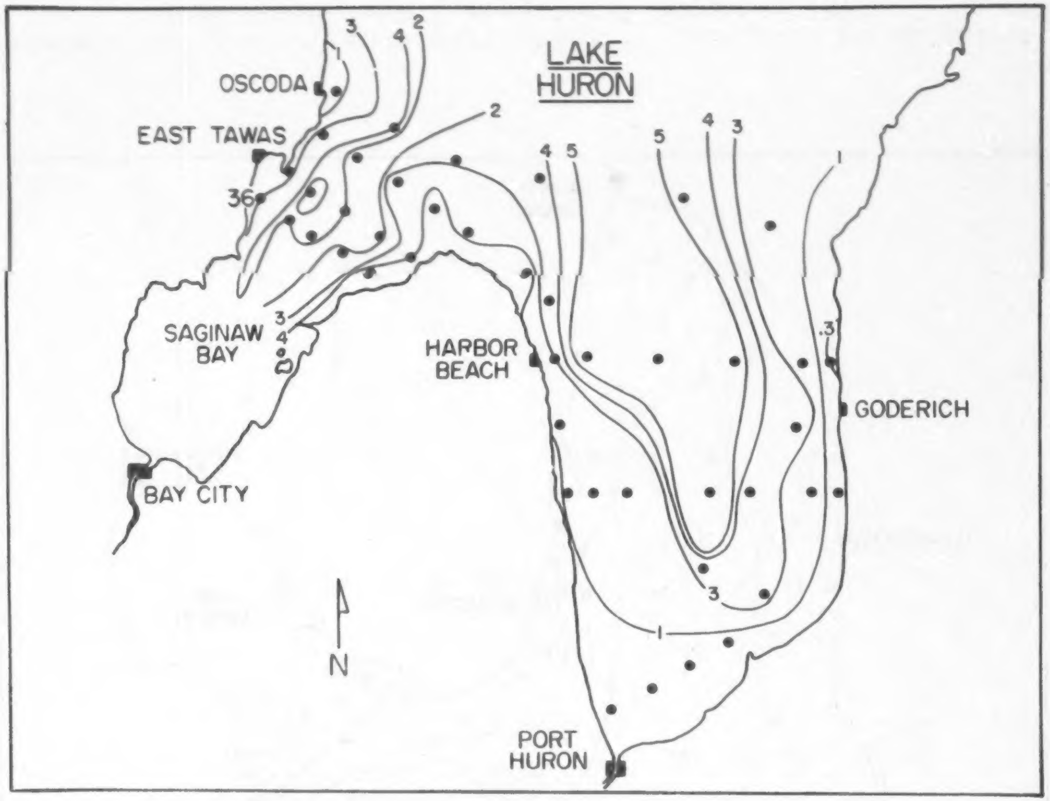
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Figure 18. Horizontal distribution of Cyclops bicuspidatus in Southern Lake Huron, 16-21 June 1974.

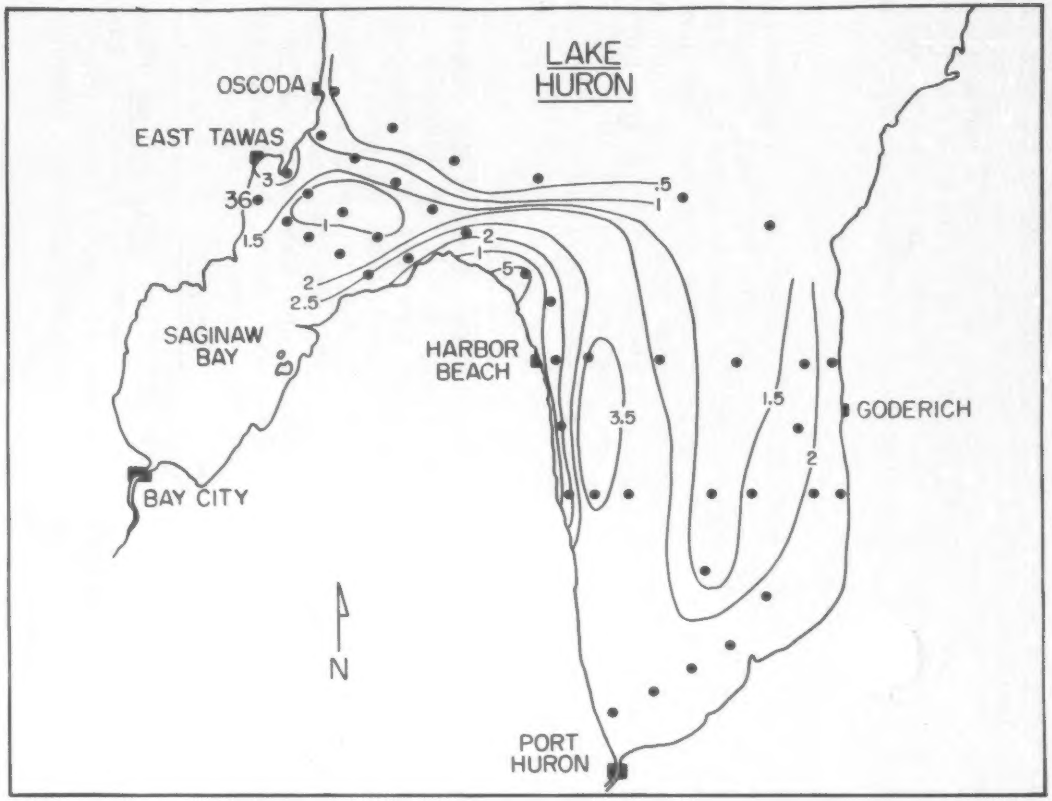
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Figure 19. Horizontal distribution of Tropocyclops prasinus in Southern Lake Huron, 10-14 November 1974.

system relationships, the areas of most intense grazing on phytoplankton, and thus, areas that could escape from biological control without such grazing.

Daphnia retrocurva--

Daphnia was commonly the most important grazer (Section 5.1) in terms of mass ingestion rate (the amount of algae consumed relative to its size). During August 1974, it was most abundant in the inshore waters of outer Saginaw Bay (Figure 20). It appears that its numbers decreased; 20,000 m^{-3} entered the Bay off Tawas, but only 2 to 5,000 m^{-3} left the Bay in water-masses that moved around the thumb of Michigan. These water-masses may move offshore in Southern Lake Huron, carrying Daphnia with them.

Eubosmina coregoni--

This relatively large bosminid (0.4 mm) was originally thought to be an oligotrophic form. In the context of current literature, it is best characterized by its relatively high susceptibility to predation in comparison with its smaller congenitor, Bosmina longirostris, which becomes dominant at high alewife densities (McNaught and Scavia, 1976). Eubosmina coregoni was most abundant inshore in outer Saginaw Bay in June 1974. It occurred in colder waters (Figure 21) and earlier in the season than B. longirostris.

Bosmina longirostris--

Eutrophic waters have been suggested where this classic indicator occurs, although it is likely a better example of an organism ideally adapted to avoid fish predation (McNaught and Scavia, 1976). Abundances of 120,000 m^{-3} were recorded in the outer waters of Saginaw Bay in June 1974 (Figure 22). As with most crustaceans, their populations spilled over around Pointe aux Barques into the main lake. Thus, the Bay is a major spring producer of Bosmina, and its production in these waters most likely influences the rest of the lake.

Holopedium gibberum--

Encased in a heavy gelatinous capsule, Holopedium floats around the lake performing as one of the most effective grazers controlling algal populations. It was slightly more abundant offshore (large areas > 4,000 m^{-3}) than immediately inshore during August 1974 (Figure 23).

Chydorus sphaericus--

As the smallest of the cladoceran grazers, Chydorus is unusually dense and often requires an algal float upon which it may rest and graze. It usually occurs concomitant with blue-green blooms, and it often exhibits high grazing rates while resting on these bouyant algae (see netplankton grazing, Section 5.2). During June 1974, Chydorus was found only in Saginaw Bay and the waters spilling around Pointe aux Barques into the

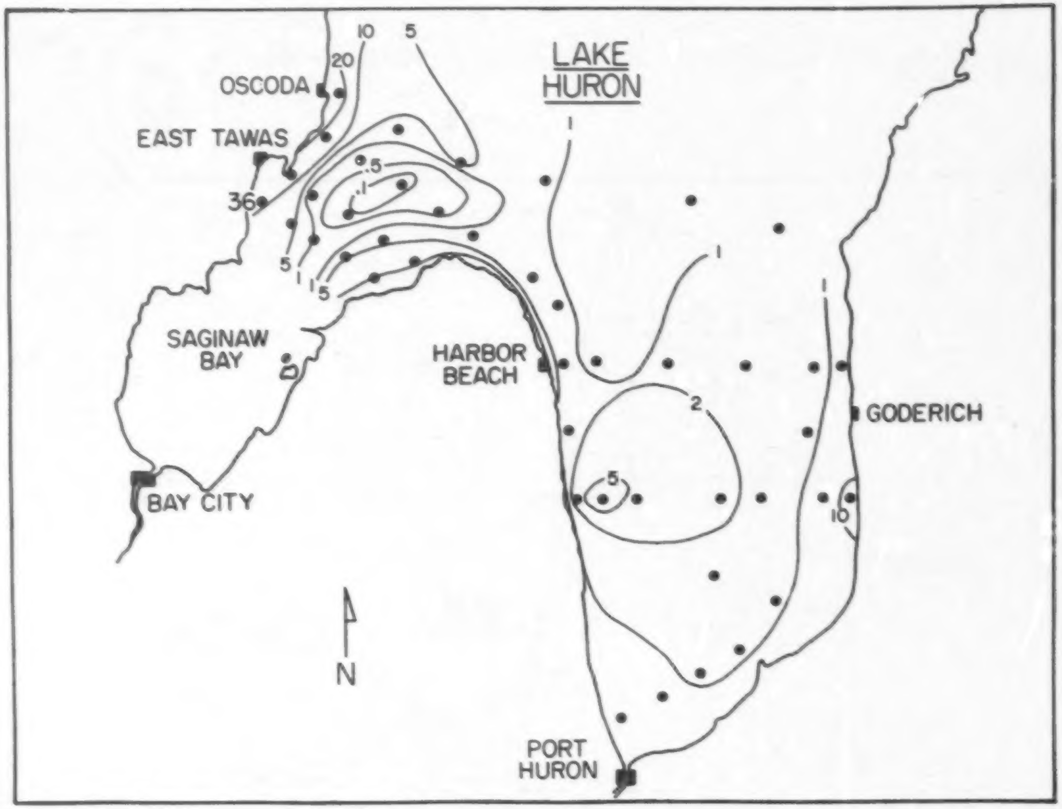
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Figure 20. Horizontal distribution of Daphnia retrocurva in Southern Lake Huron, 26-31 August 1974.

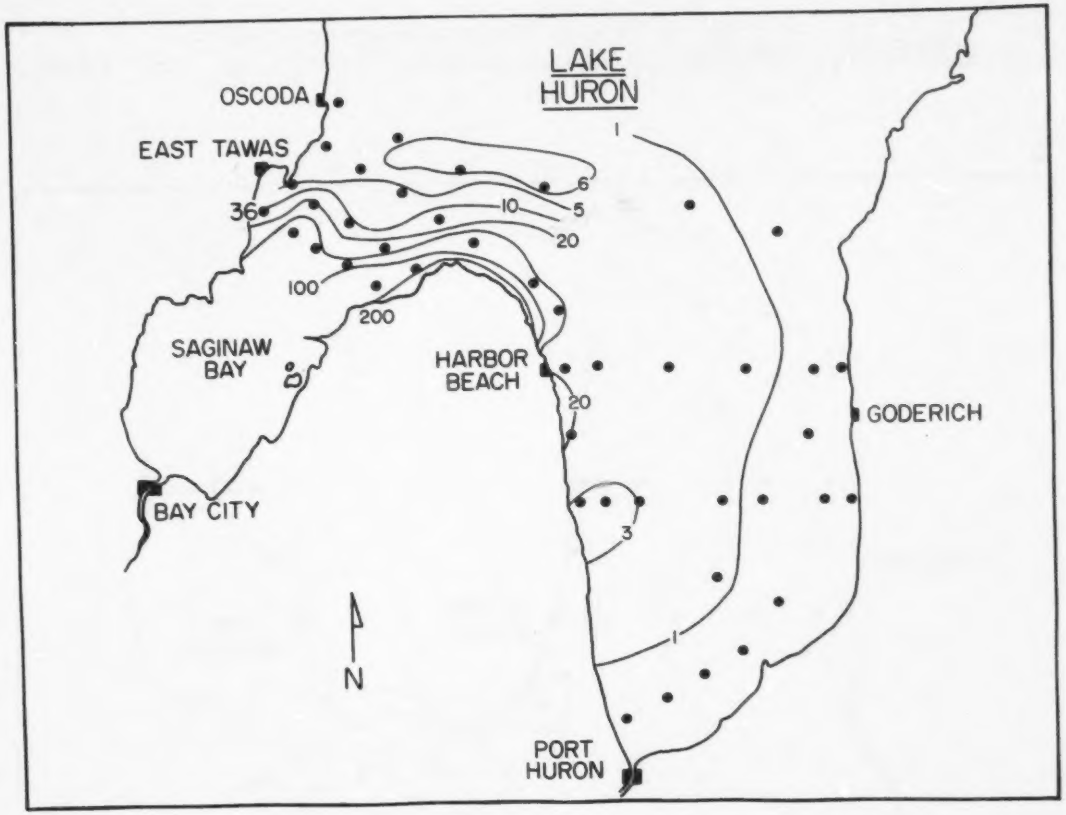
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Figure 21. Horizontal distribution of Eubosmina coregoni in Southern Lake Huron, 16-21 June 1974.

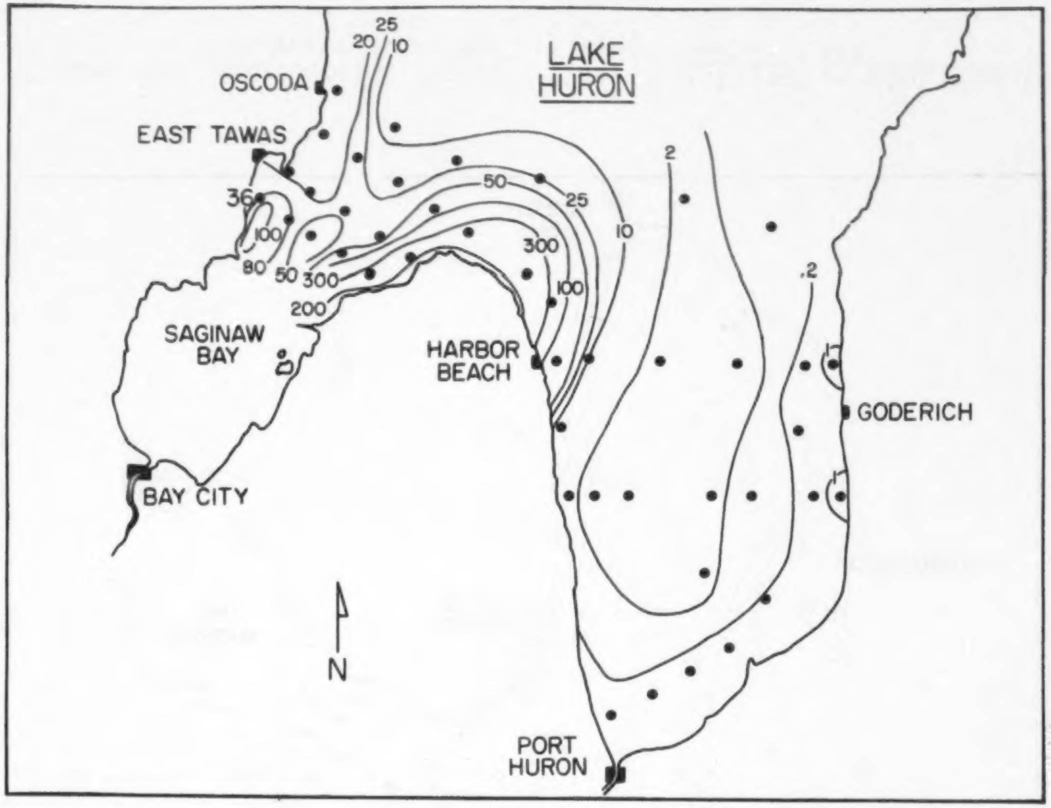
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Figure 22. Horizontal distribution of *Bosmina longirostris* in Southern Lake Huron, 16-21 June 1974.

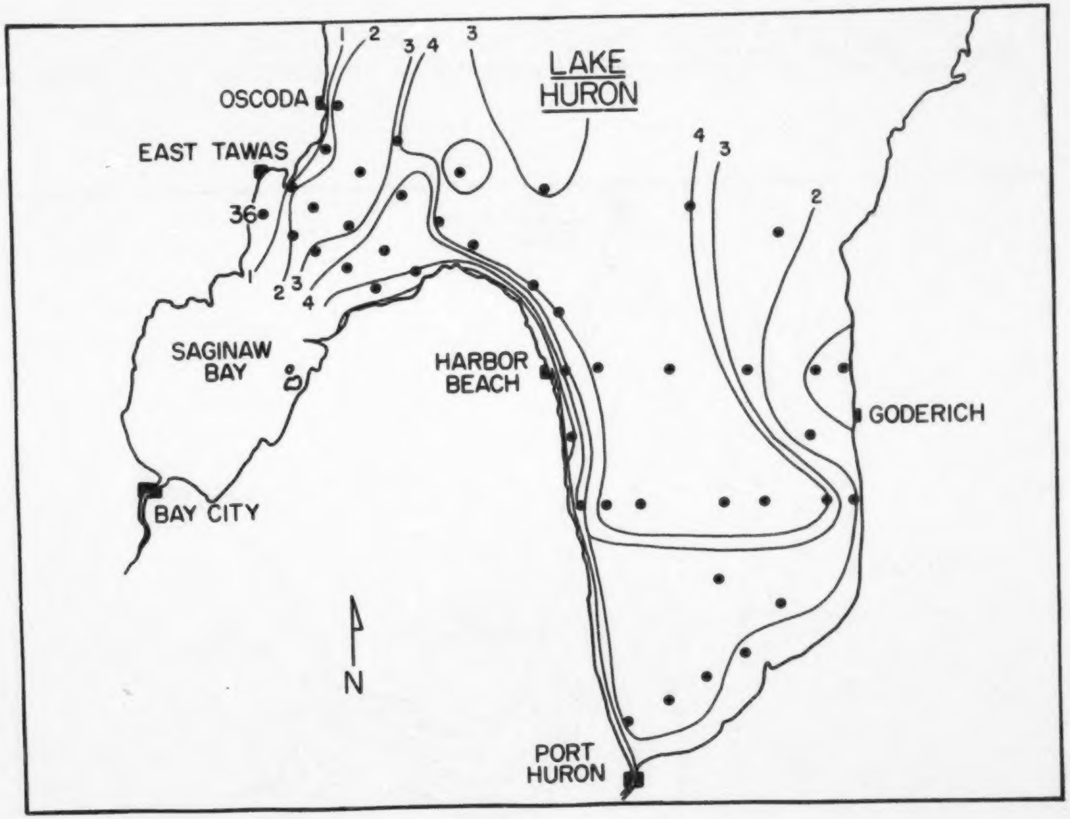
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Figure 23. Horizontal distribution of Holopedium gibberum in Southern Lake Huron, 26-31 August 1974.

Southern Main Lake (Figure 24). Certainly its distribution was correlated with the production of netplankton in the Bay.

Planktonic Ratios: An Indication of Eutrophication

Introduction--

Calanoid copepods are the most abundant crustacean zooplankton in the more oligotrophic waters of the Laurentian Great Lakes. While adults of all species of Diaptomus are only moderately abundant, their nauplii and copepodites constitute the bulk of the plankton biomass in these unproductive and usually unpolluted waters. Diaptomus sicilis, still the dominant organism in Lake Superior (Patalas 1969), is probably the original colonizer of the Great Lakes. As the most oligotrophic form, it is a useful indicator of high water quality. Trends in changing species composition have been detected from scant historical data available for crustacean populations in the Great Lakes. In Lake Ontario, the calanoid copepods decreased between 1939 and 1972, with a concomitant increase in relative numbers of the eutrophic cladoceran, Bosmina longirostris (McNaught and Buzzard, 1973). Two conclusions are warranted from this and other similar observations: high ratios of cladocerans to calanoid copepod densities are indicative of eutrophic waters, while the crustacean Bosmina longirostris is the ultimate eutrophic organism now inhabiting the Great Lakes, with an ecology in sharp contrast to the oligotrophic Diaptomus sicilis.

Use of Indicators--

To properly utilize an organism as an indicator of water quality, its total ecology should be understood. Diaptomus sicilis is here treated as an oligotrophic indicator. During our investigation of grazing in Southern Lake Huron (Sections 5.1, 5.2), we have discovered that it feeds primarily upon small nannoplankton, themselves dominant in and indicative of oligotrophic waters. Moreover, such calanoid populations are characterized seasonally by an abundance of immature nauplii and copepodites which feed almost entirely upon nannoplankton. Adult calanoids are subject to heavy fish predation, so that a lack of adults may be a sign of predation and not gross pollution. The immatures, however, are relatively immune to predation and serve as excellent indicators of unproductive waters of high quality.

At the other extreme, the cladocerans prefer warmer waters and exhibit higher growth rates. We have recently found that they consume the larger algae (greens and diatoms, but not necessarily blue-greens), thus they have access to a larger resource base in eutrophic waters. Being small at the age of maturity, they reproduce before the minimum size at which alewife predation becomes important (McNaught 1975). Since Bosmina longirostris is relatively predation-free, like the calanoid copepodites previously mentioned, its densities should reflect

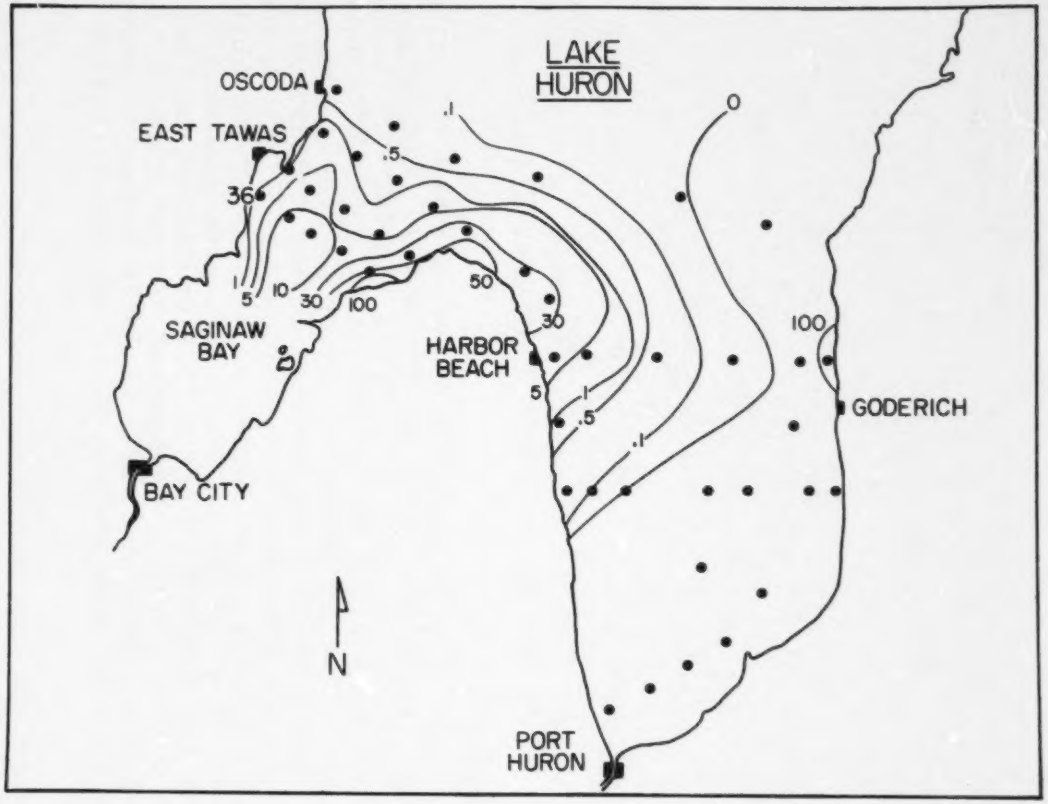
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Figure 24. Horizontal distribution of _Chydorus sphaericus_ in Southern Lake Huron, 16-21 June 1974.

the greater abundance of algal foods and the warmer temperatures of shallow, more eutrophic waters. No species or group is a perfect indicator, but we feel strongly that immature calanoids and Bosmina longirostris, two extreme forms at opposite ends of the trophic spectrum, are among the most useful indicators of pollution.

Evidence of Perturbed Areas--

During the summer of 1974, populations of Bosmina longirostris predominated in outer Saginaw Bay (Seg. 5), the nearshore waters of the Michigan coast (Seg. 4), and the offshore waters of western Lake Huron (Seg. 6) adjacent to Saginaw Bay and the forementioned coastal zone (Figure 25). Densities were lower in these areas in the spring and fall than during summer. In sharp contrast, B. longirostris was found in low numbers in northeastern offshore waters (Seg. 10), as well as in the most southernly midlake watermass (Seg. 9). But most encouraging, Bosmina was also rare along the Canadian coast (Segs. 7, 8), indicative of either the lower temperature or the higher quality of water in these areas contrasted to the Michigan coast. In contrast, Eubosmina was most abundant in Segs. 5 and 6 which is indicative of its ability to survive faster offshore (Figure 26).

Cladocerans were dominant in Southern Lake Huron during the summer months of 1974, whereas early in the spring they were common only in Saginaw Bay (Seg. 5) with densities as high as 77,000 m^{-3} (Figure 27). However, it is evident that the group has a different distribution during summertime than Bosmina. Total cladocerans were common along the eastern coastline (Segs. 7, 8), an area of the lake essentially void of Bosmina. Generally, densities of cladocerans suggest water quality problems in all areas except that northern, open lake, deep water area (Seg. 10) which never developed a significant population of these eutrophic indicators. While not lending themselves to identical conclusions, these two sets of data suggest water quality problems in Saginaw Bay and along the Michigan coast, as well as high quality water in the northern offshore watermasses (Seg. 10).

The large, brackish-water calanoid, Eurytemora affinis, is a recent invader of the Great Lakes ecosystem. Its distribution was examined with regard to areas of environmental stress, since it may have a requirement for waters of high organic content. Likewise, since it was originally adapted to more saline waters, it might be suspected of prefering polluted areas. Obviously we do not know enough about the biology of Eurytemora to carefully utilize it as an indicator. It was most abundant in Segs. 6 and 10 (Figure 28), as were total calanoid copepods (Figure 4). This finding illustrates the need for basic information on the nutritional, and reproductive, and growth aspects of each zooplankton to be used as an indicator, especially when

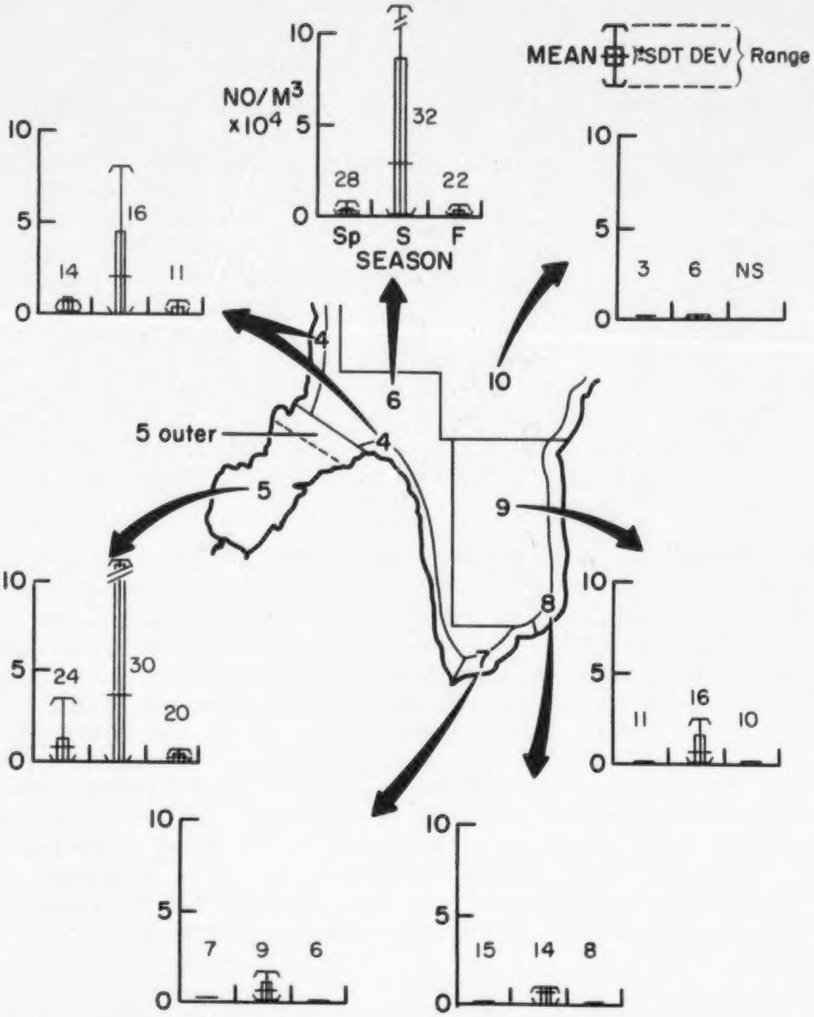

Figure 25. Mean abundance (with standard deviation and range) of _Bosmina longirostris_ in 7 segments of Southern Lake Huron during the spring (Sp), summer (S), and Fall (F) of 1974.

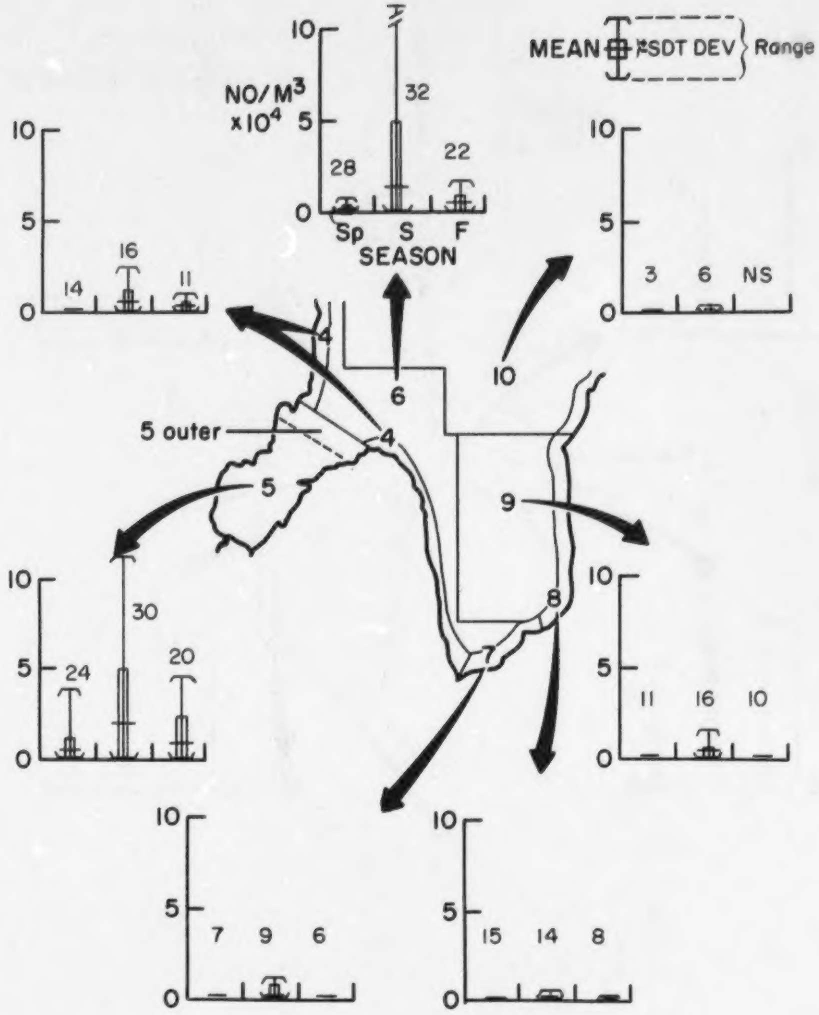

Figure 26. Mean abundance of Eubosmina coregoni in 7 segments of Southern Lake Huron during 1974.

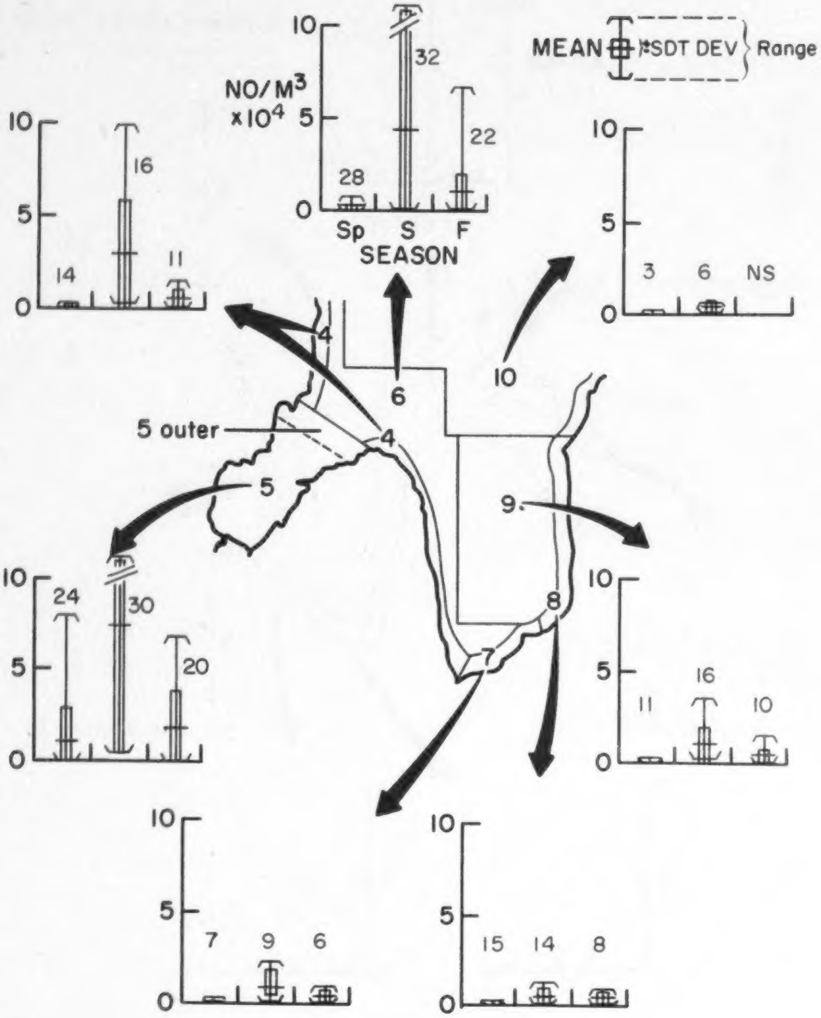

Figure 27. Mean abundance of total cladocerans in Southern Lake Huron during 1974.

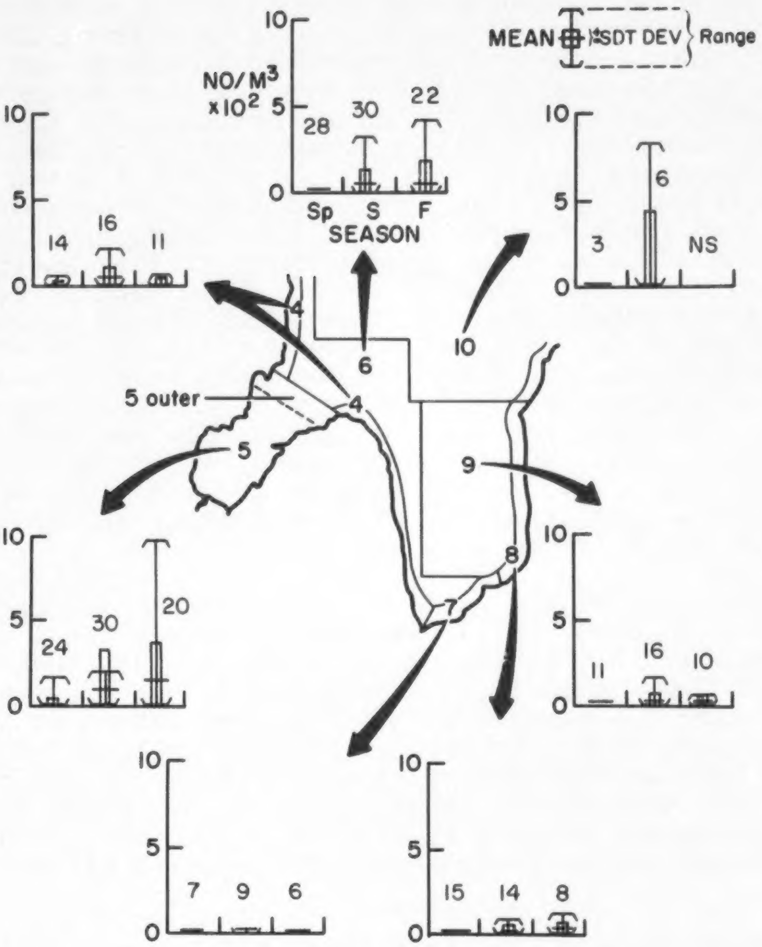

Figure 28. Mean abundance of the exotic invader *Eurytemora affinis* in Southern Lake Huron during 1974.

decisions regarding water quality have great social importance. Presently Eurytemora does not meet the criteria for such an indicator.

Evidence for Areas of High Water Quality--

It is vital to management objectives to identify those areas of Southern Lake Huron presently exhibiting high water quality. The presence of an eutrophic indicator may point to trouble, but the absence of the same organism may not indicate oligotrophic conditions. Calanoid copepods, and especially their superabundant nauplii and copepodites, are indicative of water of good quality, as opposed to cladocerans and cyclopoid copepods (Figure 29). Adult calanoids and their abundant copepodites were found in greatest numbers during the spring in Segs. 9 and 10, suspected areas of high quality water (Figure 30). They were also abundant in nearshore waters (Segs. 4, 7, 8) during the summertime. At these same times, calanoids were rare in Saginaw Bay (Seg. 5). Such populations developed in the spring, in shallow water, while these nearshore areas were cold and contained fewer of the large, eutrophic types of phytoplankton. By July, however, calanoids were excluded from inshore (Figure 30). Thus, the distribution of calalnoid copepods, as contrasted to cyclopoids (Figure 29) and cladocerans (Figure 27), suggests again that the highest quality waters in Southern Lake Huron are in Sections 9 and 10.

Information on the ratio of calanoids to cyclopoids and cladocerans (Gannon, 1977) provided us with a final overview of water quality. Due to the construction of this index, normal statistics may not apply, but comparative monthly means of this ratio (Figure 31) suggested that the deep waters of the most northerly area (Seg. 10) were of highest quality. The waters of outer Saginaw Bay (Seg. 5) and the nearshore waters of both the east and west coasts (Segs. 4, 7, 8) exhibited very similar ratios, which may reach a value of 2 during April and May when cold water calanoids predominate, but usually did not exceed unity.

In summary, all 5 indices suggested the same relative degree of eutrophication in the 7 areas of Lake Huron analyzed. Saginaw Bay was the most eutrophic, and Seg. 10 was the least productive. Generally the western coast of Lake Huron (Seg. 4) was more eutrophic than the eastern coast (Segs. 7, 8).

Evidence for Historical Trends--

Comparable data collected during 1971 and 1974 by CCIW in the main lake (apart from Georgian Bay) have been compared with regard to variations between years. The two most diagnostic groupings from our viewpoint, Bosmina longirostris alone and total calanoid copepodites and adults, have been used, and are characterized by both the seasonal mean and the standard deviation (Figure 32). Essentially, there was no evidence for in-

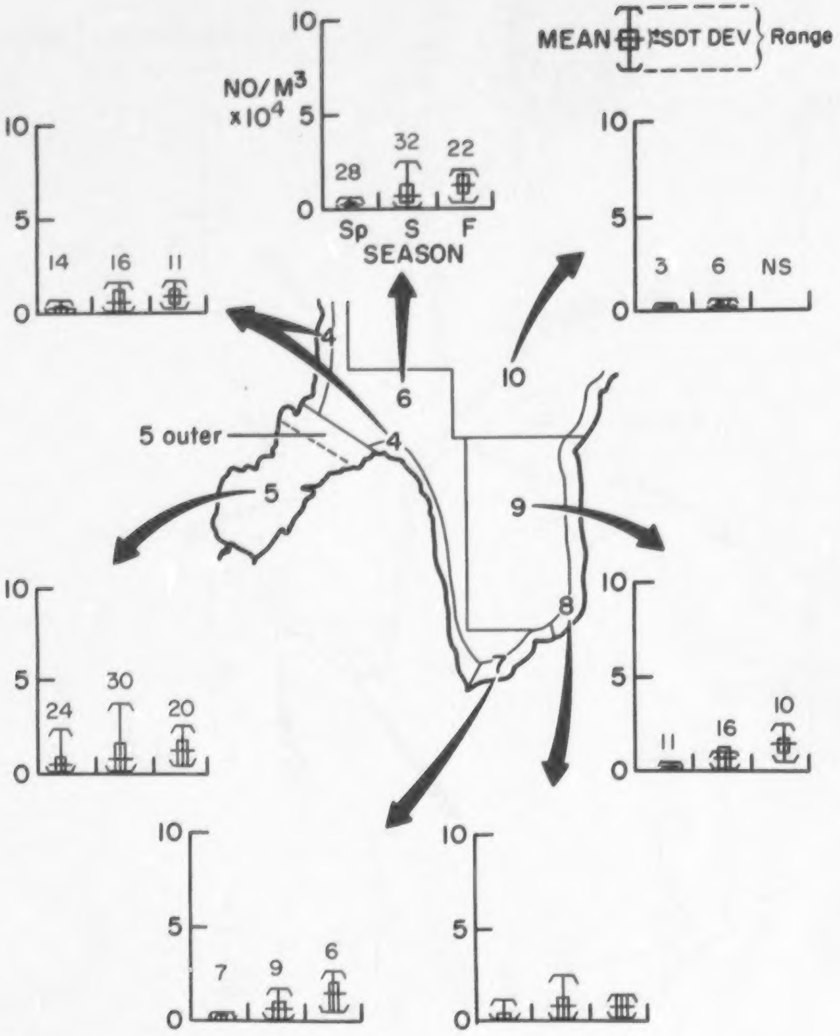

Figure 29. Mean abundance of cyclopoid copepods in Southern Lake Huron during 1974.

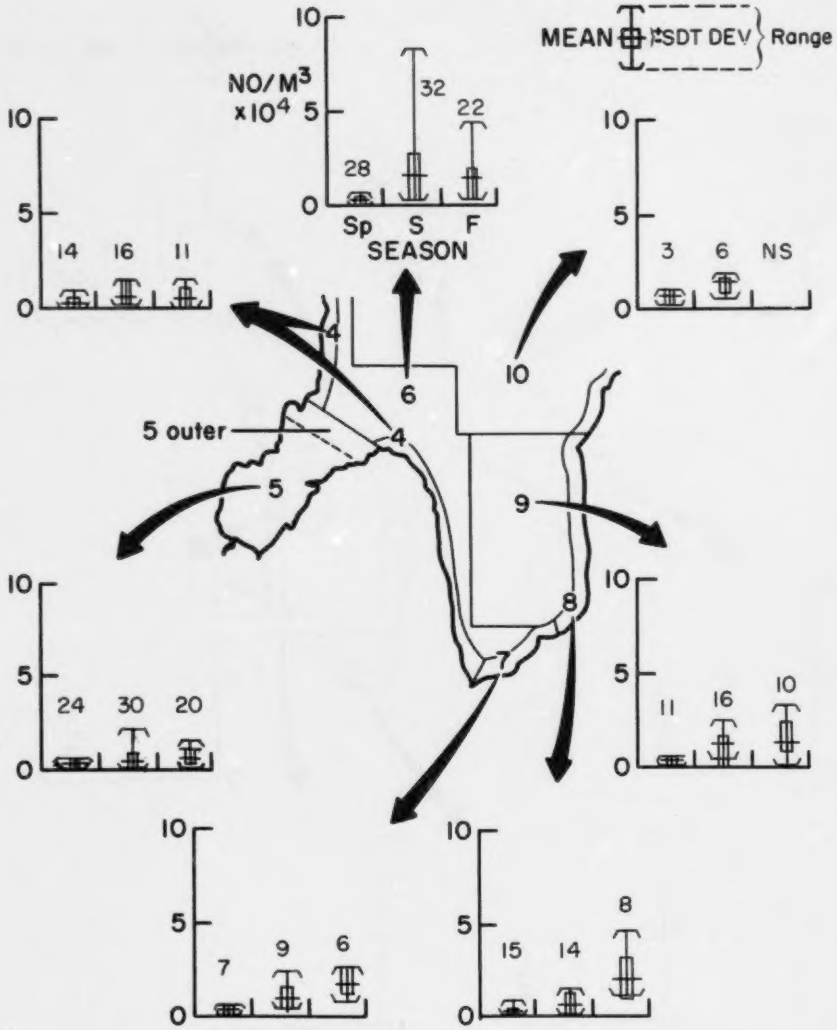

Figure 30. Mean abundance of oligotrophic calanoid copepods (predominantly copepodites) in Southern Lake Huron during 1974.

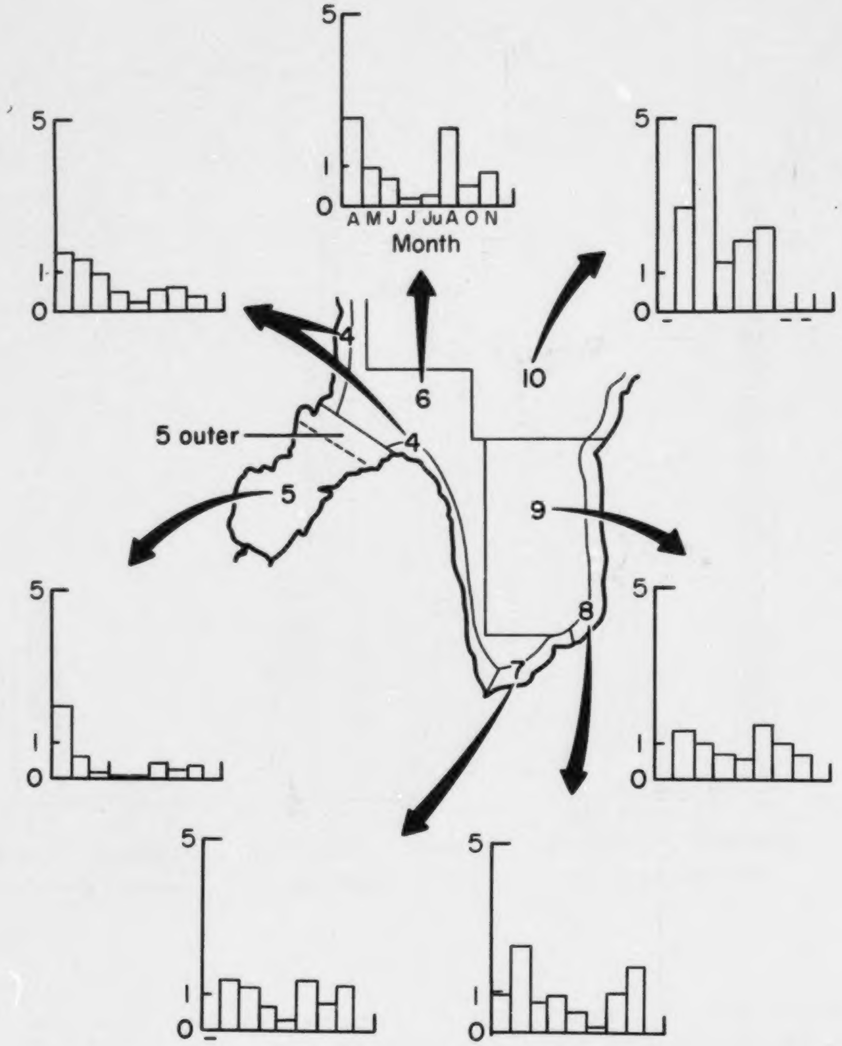

Figure 31. The ratio of calanoids to cyclopoids (adults and cops) plus cladocerans for the months April through October 1974 in Southern Lake Huron. The higher values are indicative of relatively oligotrophic conditions commonly found in segment 10.

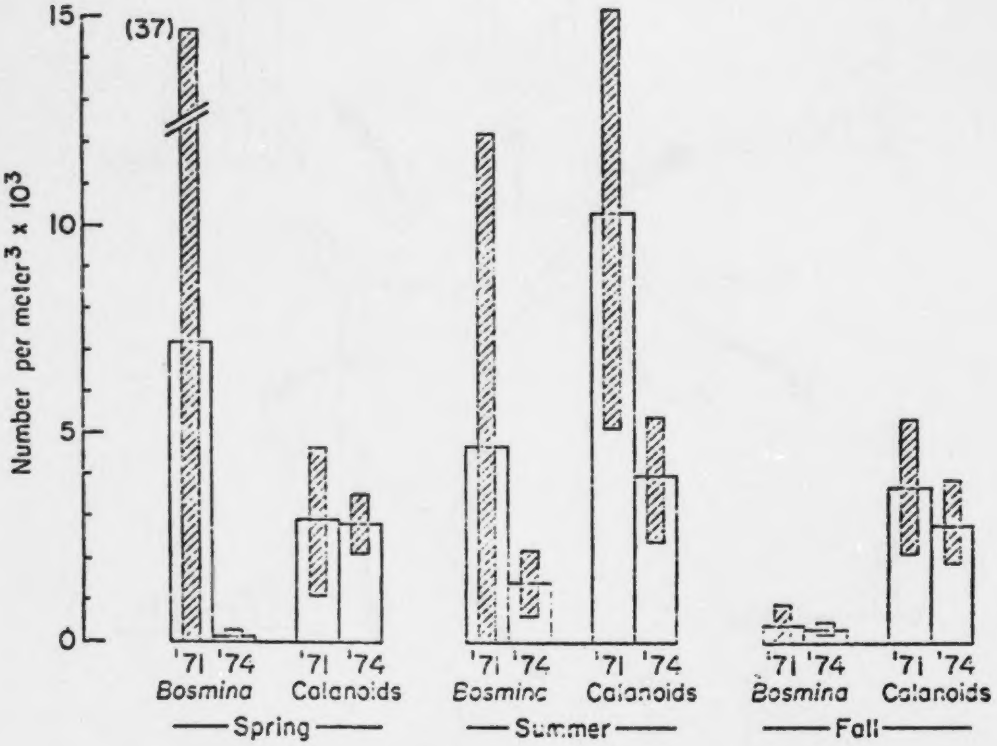

Figure 32. A comparison of populations of Bosmina longirostris and total calanoids for 1971 and 1974 for similar main lake stations (data from CCIW).

creased production of zooplankton during this brief period of 3 years between 1971 and 1974. In fact, in all cases the 1974 means were less than those for 1971. Bosmina evidently began growing later in 1974 (effect of weather?), and the seasonal mean was only 1.004 x that for 1971. Bosmina, however, characteristically has a very patchy distribution, as evidenced by large standard deviations. The calanoid copepods were less abundant in 1974 than in 1971, but in all cases the comparatively narrow standard deviations overlapped, even though calanoid standing crops in 1971 were 2.6 x more abundant than in 1974.

Certainly long-term historical trends have occurred over the 12,000 year history of Lake Huron, but we are not aware of data sets over a 50-100 year span to document such changes.

5.5 ESTIMATES OF COLUMN BIOMASS OF ZOOPLANKTON

Dry-Weights of Animals from Net Samples

The purpose of net sampling was to determine the horizontal and vertical distribution of the zooplankton by species over time. Precise estimates of dry-weight combined with densities determined in the field provided a crude estimate of the horizontal distribution of biomass by species. In contrast, the acoustic sampling results provided a good estimate of biomass, but cannot be used at the species level.

Column dry-weight biomass (mg m^{-2}) was greatest in shallow inshore waters during late April 1974 and range from a high of 0.8 to 5.1 mg m^{-2} in the mouth of Saginaw Bay to 0.9 to 1.9 mg m^{-2} off Goderich (Figure 33). Midlake biomass was very low (< 1 mg m^{-2}). This may be attributable to the low water temperatures (4.2 C) at this time. By 14-17 May 1974, column biomass was still highest inshore, ranging from 2.8 to 5.8 mg m^{-2} in outer Saginaw Bay to 2.4 to 3.8 mg m^{-2} off Goderich (Figure 34), an increase of approximately 2 x over April.

By 4-8 June 1974, the column biomass of zooplankton had increased to 5-50 mg m^{-2} in the mouth of Saginaw Bay (Figure 35). Inshore waters of the Southern Lake were uniformly 10 mg m^{-2} or greater; these inshore standing crops were 5-fold greater than those in the midlake region (2 mg m^{-2}). Eight days later (16-21 June 1974), the inshore waters were still characterized by standing crops of 10 mg m^{-2}, but the midlake waters now supported 10 to 25 mg m^{-2}, and the outer Saginaw Bay 10 to 36 mg m^{-2} (Figure 36). Throughout Southern Lake Huron, column estimates varied by a factor of 3 x (10 to 30 mg m^{-2}) and total zooplankton biomass was relatively evenly distributed (although not by species).

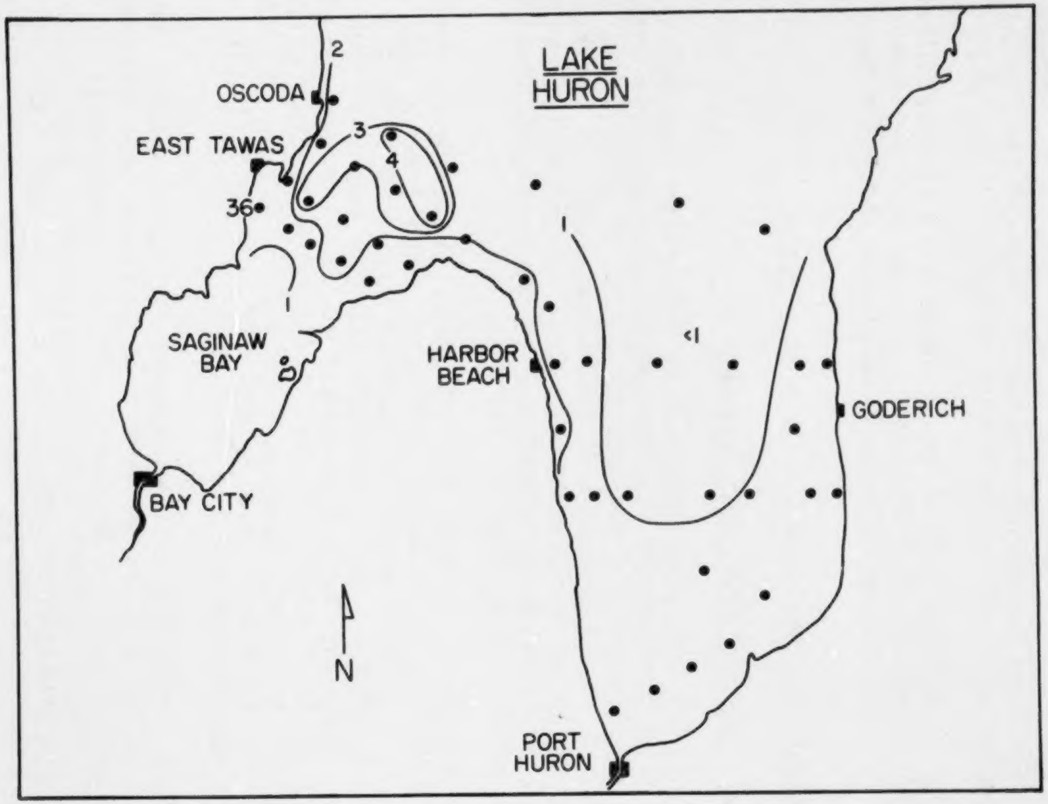
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Figure 33. Column biomass of zooplankton (mgC m^{-2}) on 28 April-3 May 1974.

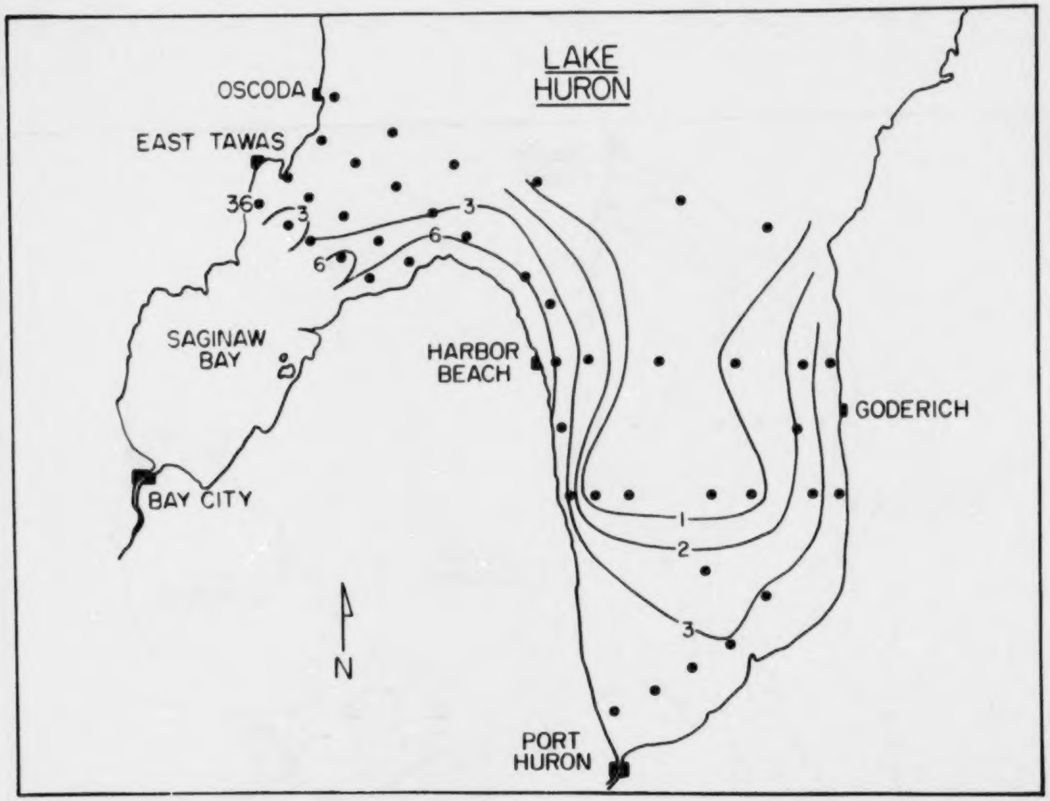

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Figure 34. Column biomass of zooplankton (mgC m^{-2}) on 14-17 May 1974.

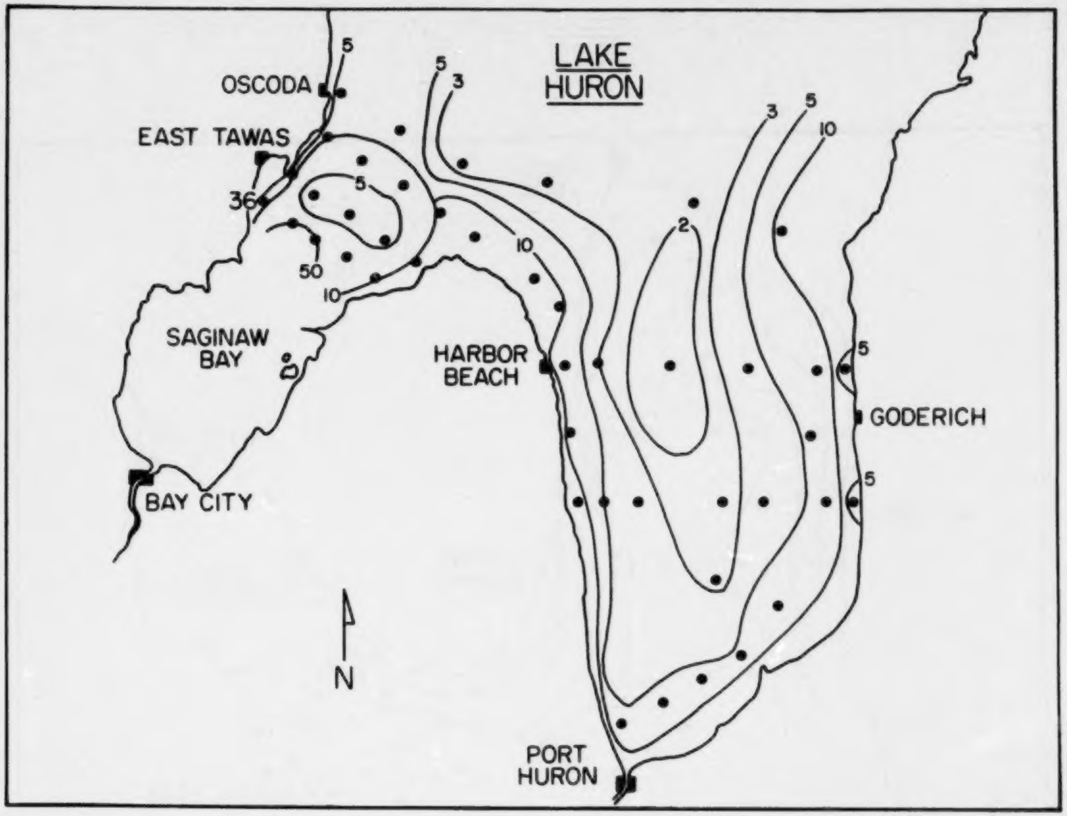
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Figure 35. Column biomass of zooplankton (mgC m^{-2}) on 4-8 June 1974.

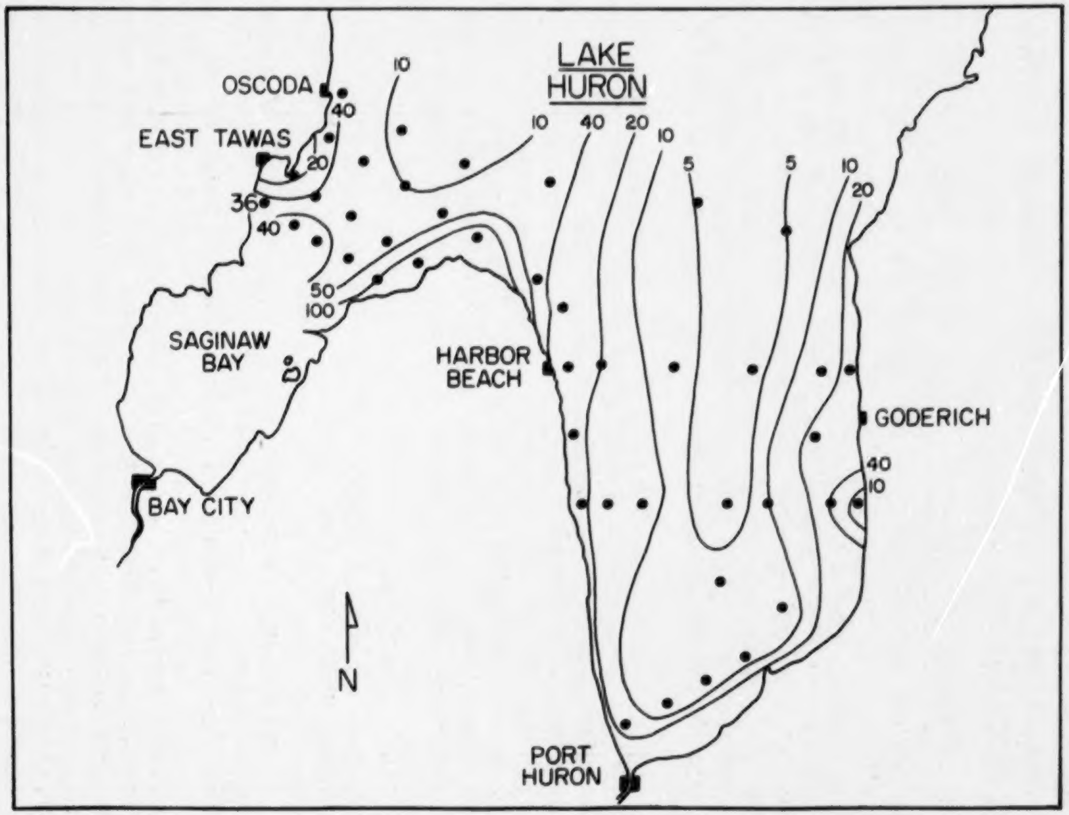
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Figure 36. Column biomass of zooplankton (mgC m^{-2}) on 16-21 June 1974.

Inshore zooplankton biomass increased markedly by 17-20 July 1975. Inshore waters of outer Saginaw Bay previously characterized by 10 to 30 mg m^{-2} in June had 20 to 100 mg m^{-2}. Biomass increased fourfold in inshore waters south of Goderich (Stations 9, 10) from 20 to 40 mg m^{-2} (Figure 37). As evidenced from an examination of counts (Appendix), deepwater biomass remained the same or decreased slightly to 5 mg m^{-2}, due to decreases in populations of copepod nauplii, *Cyclops bicuspidatus*, and *Chydorus sphaericus*.

By 26-31 August 1975 (Figure 38), large populations of zooplankton in the mouth of Saginaw Bay had crashed, falling from a range of 20 to 100 mg m^{-2} to 10 to 45 mg m^{-2}. Open water values in midlake (Stations 53, 54, 55, 21, 23) were all below 10 mg m^{-2}. However, the biomass in the extreme southern lake (south of Station 60) had increased, as evidenced by the movement offshore of the 20 mg m^{-2} isocline. Again a pocket of high standing crop was noted at Station 9, south of Goderich. This area is one where high phytoplankton productivity and nutrient levels have often been observed (Stoermer, 1978).

Fall populations (8-12 October) of zooplankton exceeded 20 mg m^{-2} only in a narrow band of waters 16 to 24 km offshore in the Southern Lake and in the deep waters of the mouth of Saginaw Bay (Figure 39). Midlake biomass had dropped to 5 mg m^{-2} by early October. By 10-14 November, the only waters to support more than 20 mg m^{-2} were in the mouth of Saginaw Bay, off Pointe aux Barques, and in the two areas of unusually high productivity which are north (Station 57) and south (Station 9, 10) of Goderich, Canada (Figure 40).

Clearly, two areas of high zooplankton production existed in Southern Lake Huron during 1974. Populations often exceeded 200 mg m^{-2} from 16 June to 14 October 1974 in the mouth of Saginaw Bay. Likewise, limited inshore populations exceeding 300 mg m^{-2} were common south of Goderich at that time. Certainly the Saginaw Bay populations were stimulated by abundant phytoplankton and detritus, resulting from nutrient enrichment. We have seen that this high secondary productivity may be carried by currents around Pointe aux Barques and may circulate further in the longshore currents. Similar observations are evident from acoustical estimates (Section 5.5). The foodchain dynamics off Goderich are based on hydrodynamic conditions which are unclear. Certainly this is an area of turbid waters, due to beach erosion and resuspension of detritus. The frequency of upwelling in this area may bring up nutrients to enrich surface waters and stimulate primary productivity. In any case, these inshore waters are often characterized by high standing crops of zooplankton.

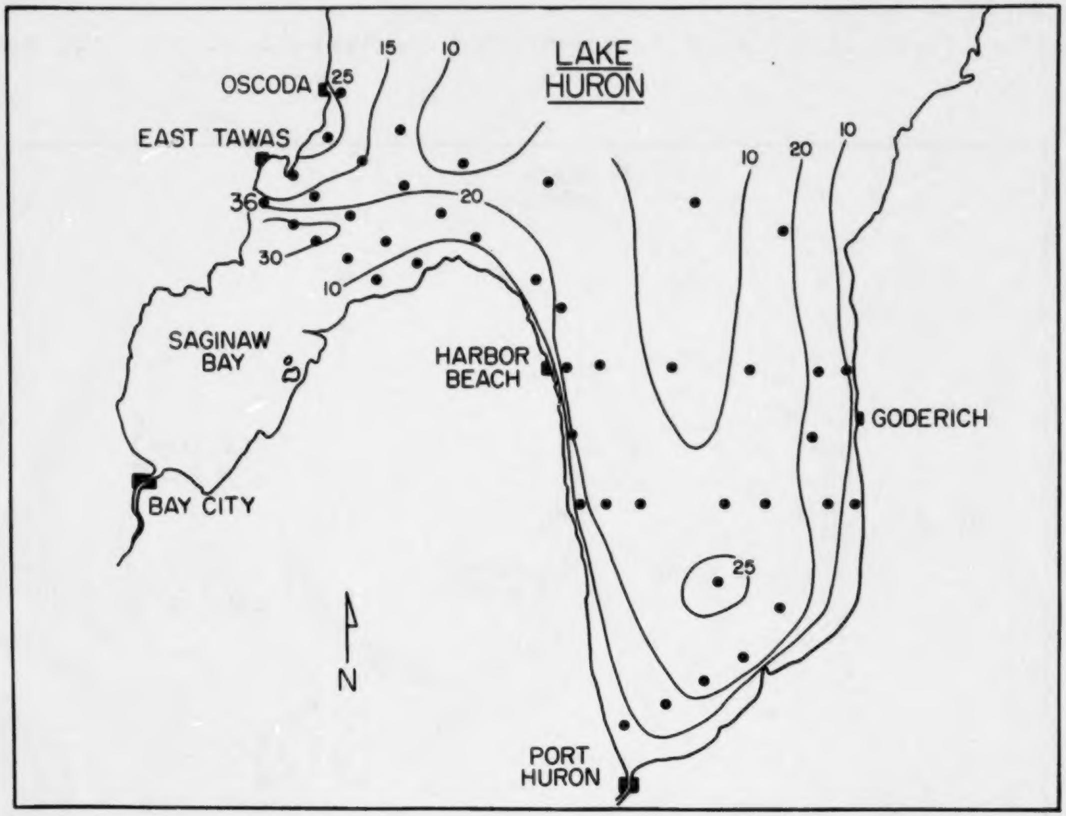

LAKE HURON
OSCODA
EAST TAWAS
SAGINAW BAY
BAY CITY
HARBOR BEACH
GODERICH
PORT HURON
25
15
10
36
20
30
10
10
20
10
25
N

Figure 37. Column biomass of zooplankton (mgC m^{-2}) on 17-22 July 1974.

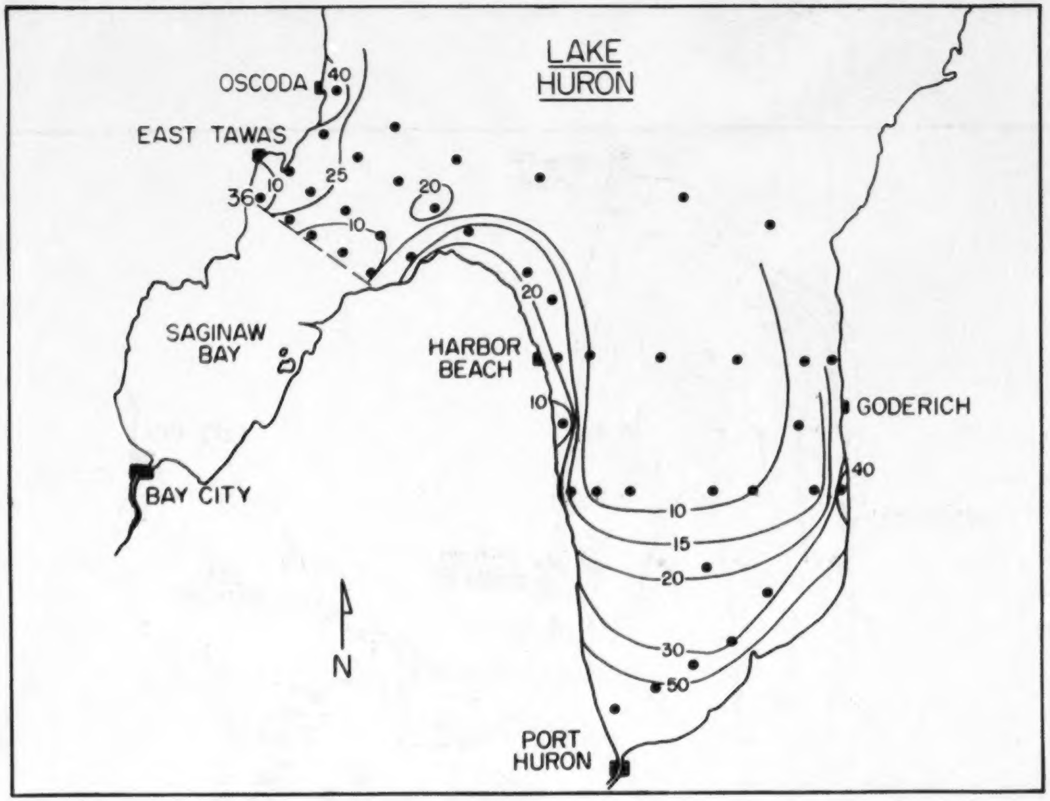
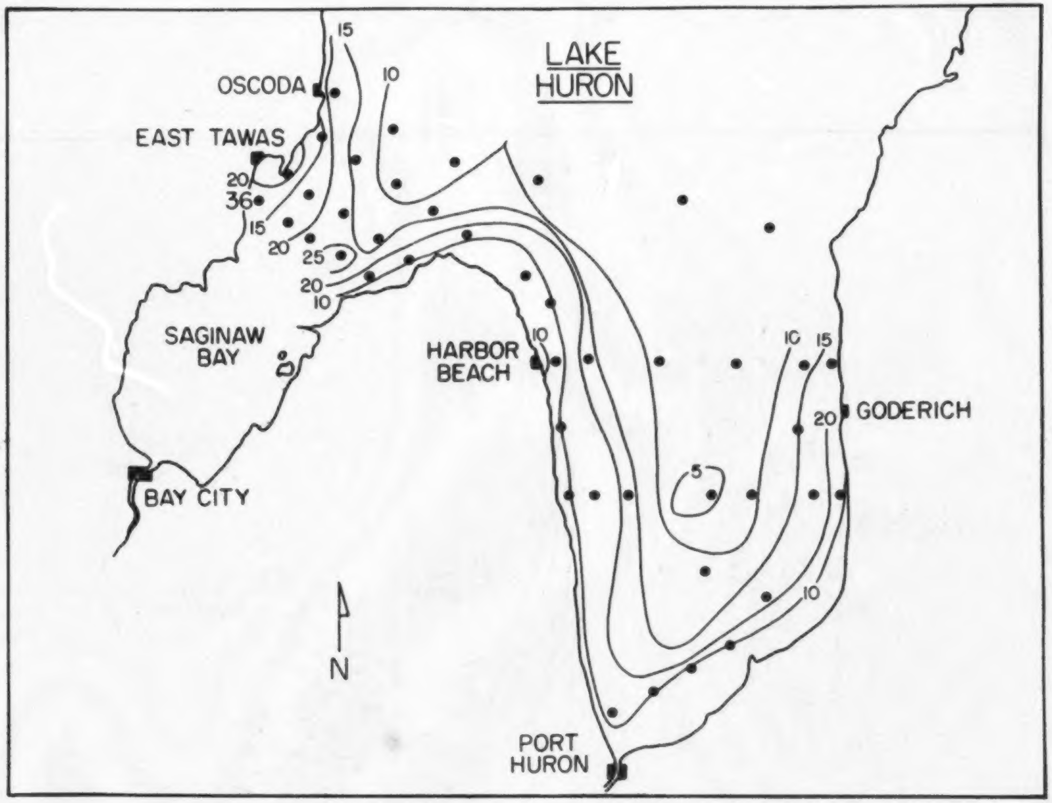

LAKE
HURON
OSCODA
40
EAST TAWAS
36
10
25
20
10
SAGINAW
BAY
BAY CITY
N
HARBOR
BEACH
20
10
GODERICH
40
10
15
20
30
50
PORT
HURON

Figure 38. Column biomass of zooplankton (mgC m^{-2}) on 26-31 August 1974.


LAKE
HURON
OSCODA
EAST TAWAS
SAGINAW BAY
BAY CITY
HARBOR BEACH
GODERICH
PORT HURON
N
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10
20
36
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15
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5
10

Figure 39. Column biomass of zooplankton (mgC m^{-2}) on 8-12 October 1974.

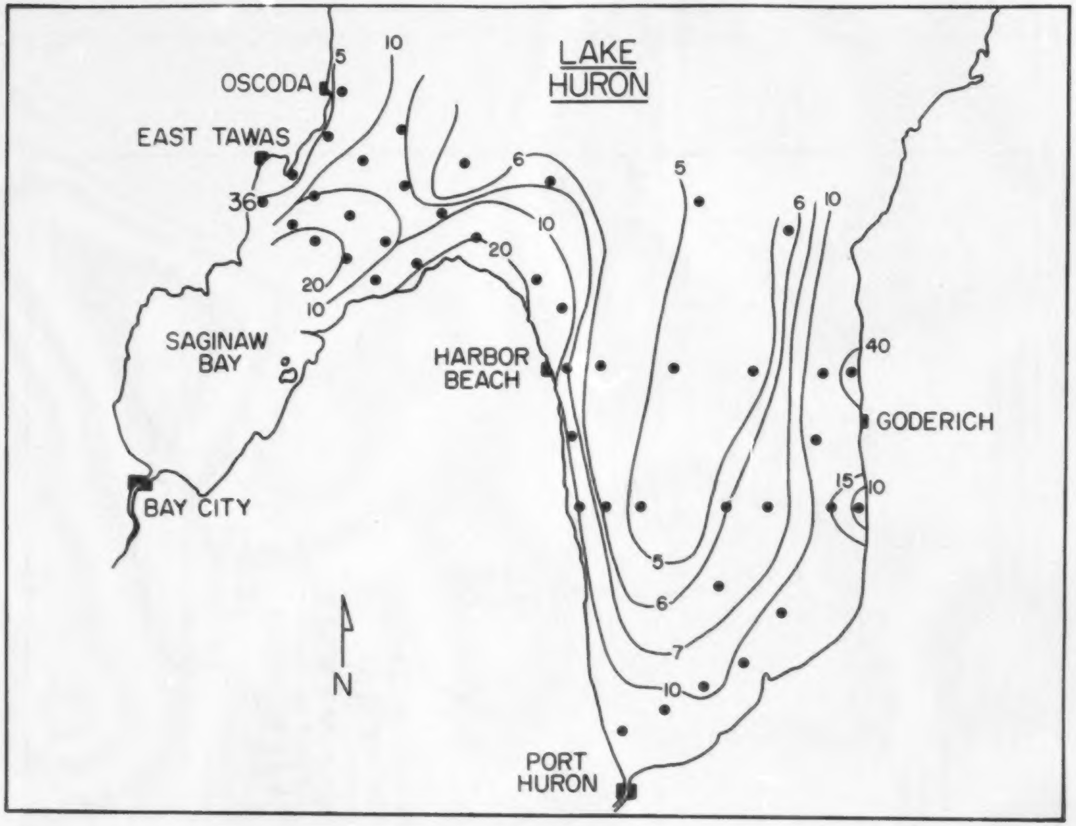
LAKE HURON
OSCODA
EAST TAWAS
SAGINAW BAY
BAY CITY
HARBOR BEACH
PORT HURON
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Figure 40. Column biomass of zooplankton (mgC m^{-2}) on 10-14 November 1974.

Acoustic Estimates of Column Biomass

One objective during the Southern Lake Huron program was to make large scale estimates of particulate biomass, both throughout the water column at each station, and over the sampling end of 43 stations (see Maps, Figure 41-43).

Areal Estimates of Acoustical Biomass--

Applied Great Lakes ecology requires the estimation of secondary production with regard to the location, primary productivity, and associated degree of nutrient enrichment of an area. Acoustical estimates of particulate biomass may serve as an integrated estimate of the standing stock of particulate organic carbon (POC), and at least in shallow waters, of the standing crop (in a column) of zooplankton within a prescribed size-range. Routine surveillance studies of the Great Lakes require that research vessels visit a prescribed series of stations on a regular basis. The deployment of a specially constructed particle counter has permitted us to make routine particle surveys. Since resource management can best utilize data collected over a broad geographic scale, we will present monthly and seasonal summaries of column particle abundance on an areal basis (mgC m^{-2}).

Seasonal Summary of Acoustical Biomass--

Acoustic estimates of total particle biomass for all particle sizes exhibited two maxima in Southern Lake Huron, one in early June and the other in August (Table 27). The ready division of particles into size classes is one of the major advantages of our custom-built sonar (McNaught *et al.*, 1975). For the purposes of this analysis of plankton, the total particle spectrum was divided into three size classes, with the smallest classes (0.8 to 2 mm and 2 to 3 mm) including the zooplankton, and the largest class (3 to 5 mm) including the remaining biomass. Acoustical returns converted to biomass, and thus representative of the small size-class biomass (mgC m^{-3}), also show maxima in June (691.9 mgC m^{-3}) and August (190.8 mgC m^{-3}). From earlier detailed analysis of data from Lake Ontario (McNaught, unpublished), we know that most of the particles in the appropriate range for zooplankton (.08 to 2 mm) are indeed zooplankton if located within the upper 40 m of the water column, but that other very significant echoes have been detected from below 50 m, probably from aggregates of particulate organic matter. Thus, while the mean acoustic biomass shows seasonal patterns which, like the biomass estimates from net sampling, are bimodal, these acoustic estimates are certainly high if interpreted as representing only zooplankton. Acoustic estimates (on a volume basis) have compared with biological net sampling estimates from the same stations (Table 28) to provide an idea of how often over estimation may have occurred (about 33% of the time).

TABLE 27. BIOMASS (mgC m^{-3}) OF ZOOPLANKTON AND OTHER PARTICLES PER UNIT VOLUME (m^{-3}) DETERMINED ACOUSTICALLY WITHIN SIZE-CLASS (0.8 to 2 mm and 2 to 3 mm)

			Biomass (mgC m^{-3})	
Date	Number Stations	0.8-2 mm	2-3 mm	All Sizes
April-May 1974	22	169.5	206.8	376.3
14-17 May 1974	21	129.1	155.3	284.4
4-8 June 1974	18	691.9	442.2	1134.1
16-21 June 1974	32	62.7	45.4	108.1
August 1974	18	190.8	503.5	694.3
October 1974	33	83.6	189.1	272.7
November 1974	37	99.9	220.5	320.4
6-10 August 1975	7	77.4	152.5	229.9
17-23 October 1975	7	98.9	54.3	153.2

TABLE 28. COMPARATIVE BIOMASS OF ZOOPLANKTON (0.8 to 2 mm) ESTIMATED BY ACOUSTICS AND FROM NET SAMPLES IN SOUTHERN LAKE HURON, 1974-75

Date	Acoustic Estimate, Zooplankton Biomass ($mgC\ m^{-3}$)	Net Estimate, Dry Weight ($mgC\ m^{-3}$)
28 April-3 May 1974	169.5	31.8
14-17 May 1974	129.1	68.5
4-8 June 1974	691.9	135.6
16-21 June 1974	62.7	457.2
17-22 July 1974		354.3
26-31 August 1974	190.8	311.3
8-12 October 1974	83.6	273.1
10-14 November 1974	99.9	179.3
6-10 August 1975	77.4	151.9
17-23 October 1975	98.9	141.4

June 1974 (0.8 to 2 mm particles)--

Large densities of zooplankton and other particles were frequently observed on sonar. Often they were associated with longshore currents that were leaving Saginaw Bay around Pointe aux Barques and flowing southeast past Harbor Beach. During June 1974, the main concentrations of particulate biomass were seen specifically in watermasses leaving Saginaw Bay and in the deeper waters of Goderich (Figure 41). Generally biomass levels in Southern Lake Huron south of a line from Port Sanilac east to the Canadian Shore were below 100 mgC m^{-2}. However, in watermasses leaving Saginaw Bay that exceeded 100 mgC m^{-2}, considering that these are shallow waters average only 25 m depth, the mean volume biomass can be estimated to exceed 4 mgC m^{-3}. Most of it was likely zooplankton. In the deep hole off Goderich, the column biomass exceeded 100 mgC m^{-2}, but the mean volume biomass was only about 1.2 mgC m^{-3}, since the mean depth is approximately 85 m. Most of the biomass off Goderich was in deep water and was probably detrital in nature.

October 1974 (0.8 to 2 mm particles)--

During October 1974 high particle densities were observed in the mouth of Saginaw Bay (> 200 mgC m^{-2}), whereas in the main lake densities above 100 mgC m^{-2} they were not observed south of a line from Port Sanilac east to Canada. Generally the northerly stations in midlake and along the Canadian shore were not sampled, due to changes in cruise scheduling, and this is indicated on the map (Figure 42). Particle densities entering Saginaw Bay in the longshore currents off East Tawas were below 100 mgC m^{-2}, whereas those exiting Saginaw Bay around the thumb were greater than 200 mgC m^{-2}. One shallow station (Station 16) reached 487 mgC m^{-2}. Again, similar evidence indicated that Saginaw Bay was a productive area generating zooplankton and detritus and was then spilling this secondary productivity into the shoreward waters of the main lake. However, with the intensity of sampling available it is difficult to estimate to what degree Saginaw Bay enriches the main lake with populations of zooplankton and quantities of organic particulate matter. Certainly the earlier growth in the warmer waters of the Bay may act to seed the open lake with adult cladocerans. Such aggregations of zooplankton entering the open lake may also increase the biological control on phytoplankton through grazing, if those local phytoplankton populations are relatively nutrient-limited.

November 1974 (0.8 to 2 mm particles)--

The areal biomass (mgC m^{-2}) for November 1974 showed a high standing crop in the mouth of Saginaw Bay (Figure 43). There were clumps present which ranged in concentration from 22 to 594 mgC m^2. Thus, integrated column biomass was high in the area of the mouth of Saginaw Bay, but was characterized by high heterogeneity or spatial variability. Only a few stations were visited in the main lake. In this area south of a line from

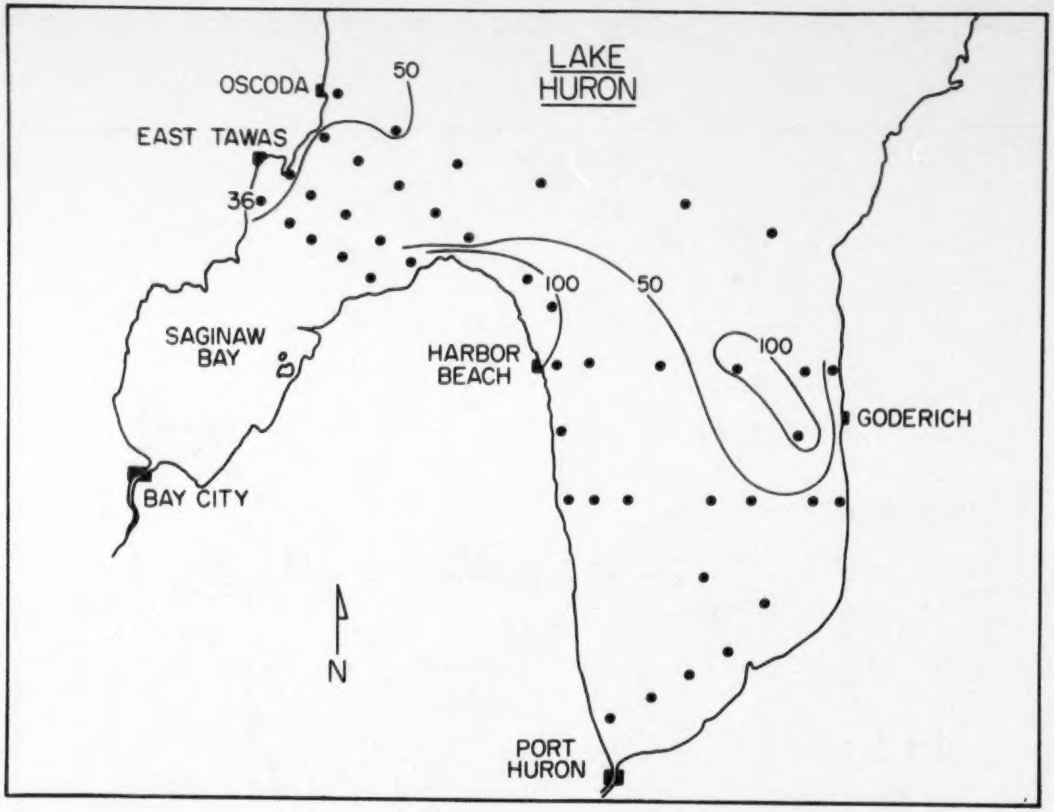
LAKE HURON
OSCODA
EAST TAWAS
36
50
SAGINAW BAY
BAY CITY
HARBOR BEACH
100
50
100
GODERICH
PORT HURON
N

Figure 41. Acoustic column biomass (mgC m^{-2}) on 16-21 June 1974.

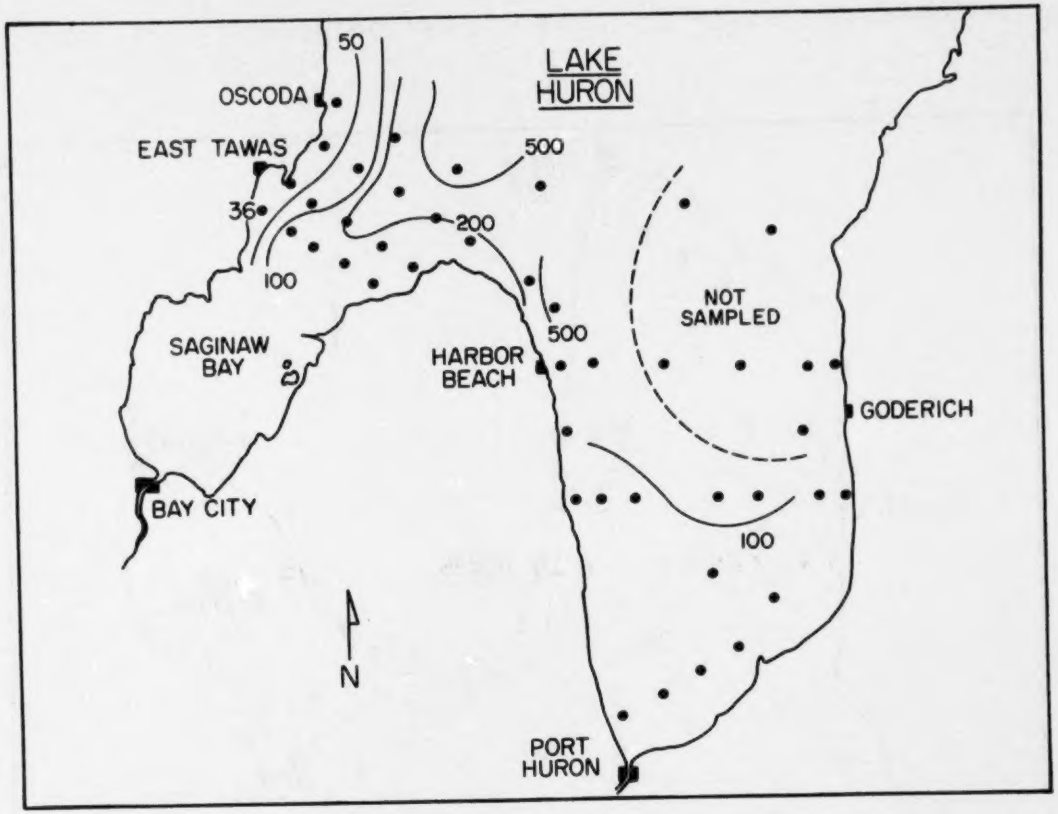
LAKE HURON
50
OSCODA
EAST TAWAS
36
100
500
200
500
NOT SAMPLED
SAGINAW BAY
HARBOR BEACH
GODERICH
BAY CITY
100
N
PORT HURON

Figure 42. Acoustic column biomass (mgC m^{-2}) on 8-12 October 1974.

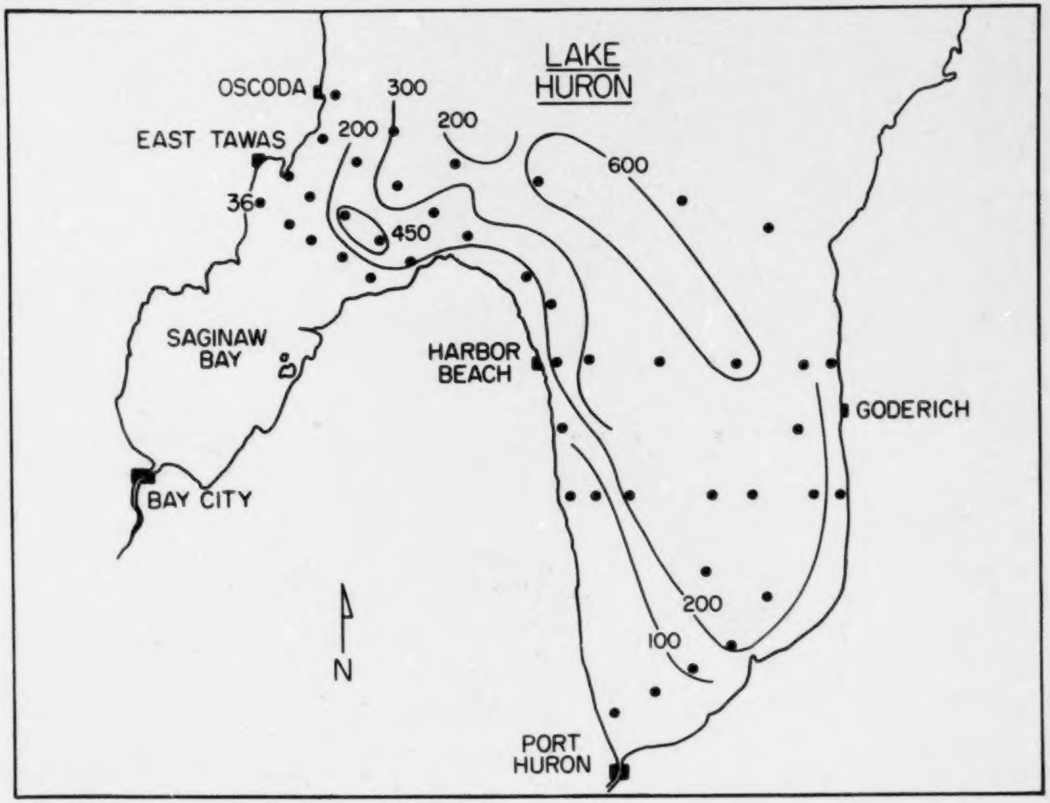
LAKE HURON
OSCODA
EAST TAWAS
36
300
200
200
600
450
SAGINAW BAY
HARBOR BEACH
GODERICH
BAY CITY
N
200
100
PORT HURON

Figure 43. Acoustic column biomass (mgC m^{-2}) on 10-14 November 1974.

Oscoda to Kincardine, the column biomass was high for deep stations and low for inshore stations; most likely an indication that it was strongly influenced by the deep detrital biomass and not the zooplankton component. A secondary conclusion suggested that Saginaw Bay provides a large biomass of zooplankton and other large particles, which again are transported by watermasses moving around Pointe aux Barques and then flowing in a southeast direction along the shore of the thumb of Michigan. This conclusion is in part based on a conversion of areal biomass to unit volume biomass, obviously since the highest column biomass occurred in the midlake region.

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APPENDIX A

Lakewide Abundance of Zooplankton (mean density)

Numbers are corrected for net efficiency for each depth interval; to obtain raw data divide by constants as follows: (0-5, 1.67; 0-10, 1.78; 0-20, 2.00; 0-40, 2.17).

TABLE 29. LAKEWIDE ABUNDANCE OF ZOOPLANKTON POPULATION DENSITIES ($\# \ m^{-3}$) FOR THE WATER COLUMN FIVE METERS TO SURFACE

Species	28-03 Apr	14-17 May	04-08 June	16-21 June	17-22 July	26-31 Aug	08-12 Oct	10-14 Nov	02-13 Apr	28-31 May	6-10 Aug	17-23 Oct
Cladocera												
Leptodora	0	0	0	0	62	450	81	4	0	0	136	23
Eubosmina coregoni	27	55	38	29166	7132	4774	10507	4043	128	16042	11932	6138
Bosmina longirostris	15	35	155	97917	142725	3511	2768	851	5	8883	6144	1955
Daphnia retrocurva	0	0	1	1547	1385	3780	1649	50	0	189	9024	780
Daphnia galeata	2	5	3	49	9	749	4348	2056	29	22	1070	1625
Daphnia longiremis	3	0	0	0	0	7	1	63	0	0	19	0
Ceriodaphnia lacustris	0	0	0	0	25	178	14	0	0	0	1050	1
Chydorus sphaericus	0	0	0	14165	1815	2202	3333	1876	30	228	1588	2924
Holopedium gibberum	0	0	0	20	434	2541	1744	292	0	115	6023	927
Diaphanosoma leuch.	0	0	0	0	0	7	2	0	0	0	19	0
Polyphemus pediculus	0	0	0	0	116	98	0	0	0	0	285	0
Alona spp.	0	0	0	0	0	0	15	201	0	0	0	0
Cyclopoida												
Copepodites	963	550	3243	24709	10610	5134	16366	18171	1037	8175	9045	13680
Cyclops bicuspidatus(F)	648	503	302	864	309	295	567	455	663	438	357	236
Cyclops bicuspidatus(M)	339	454	98	1395	378	81	378	511	489	239	247	152
Cyclops vernalis(AD)	14	0	0	58	0	35	158	165	13	28	186	159
Cyclops vernalis(IM)	2	0	0	112	384	366	630	360	3	110	993	305
Tropocyclops	9	40	4	298	66	1313	1714	1015	10	0	1106	1171
Tropocyclops	0	70	0	68	0	885	219	29	0	0	411	31
Mesocyclops edax(AD)	2	0	0	0	0	66	30	1	3	11	111	11
Mesocyclops edax(IM)	0	0	0	0	0	201	532	162	0	0	442	275
Copepod Nauplii	.16273	26296	20517	39220	22934	22976	17712	17547	25969	29669	28322	6468
Calanoida												
Copepodites	475	2716	2604	10759	7363	17901	19819	11848	84	3897	9923	7510
Diaptomus ashlandi(F)	298	262	80	148	101	38	43	99	902	223	58	21
Diaptomus ashlandi(M)	312	60	74	79	63	32	39	365	989	246	56	63
Diaptomus sicilis(F)	145	65	35	70	425	3	40	1149	520	172	0	24
Diaptomus sicilis(M)	98	166	67	90	567	0	8	907	619	303	5	23
Diaptomus minutus(F)	206	287	163	251	0	2077	196	2055	867	1731	1687	80
Diaptomus minutus(M)	214	161	168	148	0	1822	158	1314	722	3277	1813	76
Diaptomus oregonensis(F)	53	10	8	38	0	159	82	614	64	19	83	30
Diaptomus oregonensis(M)	27	10	8	9	51	162	104	343	48	0	105	40
Limnocalanus macrurus(AD)	10	20	0	0	0	3	2	31	21	28	4	0
Limnocalanus macrurus(IM)	51	40	6	43	0	5	59	1	4	0	0	0
Eurytemora affinis(AD)	0	0	0	0	0	7	19	19	0	11	45	22
Eurytemora affinis(IM)	0	0	7	20	0	34	97	29	0	0	101	8
Epischura lacustris(AD)	0	0	0	0	0	84	127	47	0	0	48	133
Epischura lacustris(IM)	0	0	34	13	240	629	255	14	0	0	131	49
#Station	8	2	5	7	4	33	33	41	17	3	14	14

TABLE 30. LAKEWIDE ABUNDANCE OF ZOOPLANKTON POPULATION DENSITIES ($\# \ m^{-3}$) FOR THE WATER COLUMN TEN METERS TO SURFACE

Species	28-03 Apr	14-17 May	04-08 June	16-21 June	17-22 July	26-31 Aug	08-12 Oct	10-14 Nov	02-13 Apr	28-31 May	6-10 Aug	17-23 Oct
Cladocera												
Leptodora	-	0	0	0	0	14	19	0	0	0	-	7
Eubosmina coregoni	-	10	194	1327	2088	320	1201	506	0	0	-	595
Bosmina longirostris	-	1	68	1981	6141	429	691	300	0	0	-	81
Daphnia retrocurva	-	0	0	11	123	397	1111	7	0	0	-	257
Daphnia galeata	-	7	2	53	73	1116	1476	764	0	95	-	630
Daphnia longiremis	-	2	0	0	0	7	0	0	0	0	-	0
Ceriodaphnia lacustris	-	0	0	0	2	8	0	0	0	0	-	0
Chydorus sphaericus	-	0	4	124	29	0	161	79	0	0	-	49
Holopedium gibberum	-	0	1	0	90	825	536	0	0	0	-	207
Diaphanosoma leuch.	-	0	0	0	0	1	3	9	0	0	-	0
Polyphemus pediculus	-	0	0	0	5	1	0	0	0	0	-	0
Alona spp.	-	0	0	0	0	0	0	0	0	0	-	0
Cyclopoida												
Copepodites	-	435	769	5784	11922	5231	7055	8124	0	672	-	6915
Cyclops bicuspidatus(F)	-	587	842	1417	783	358	302	224	0	368	-	101
Cyclops bicuspidatus(M)	-	273	358	1054	128	135	219	160	0	25	-	80
Cyclops vernalis(AD)	-	3	3	0	5	1	10	36	0	0	-	24
Cyclops vernalis(IM)	-	0	1	0	7	4	103	102	0	0	-	191
Tropocyclops	-	13	22	26	21	162	547	258	0	0	-	361
Tropocyclops	-	4	3	0	0	160	73	15	0	0	-	172
Mesocyclops edax(AD)	-	0	0	0	8	87	10	0	0	0	-	24
Mesocyclops edax(IM)	-	0	3	21	0	117	153	22	0	0	-	155
Copepod Nauplii	-	5852	15107	25598	25952	28255	10995	7276	0	30728	-	7768
Calanoida												
Copepodites	-	298	1085	10560	12389	6224	10378	6043	0	2703	-	4749
Diaptomus ashlandi(F)	-	273	238	389	103	68	26	170	0	390	-	11
Diaptomus ashlandi(M)	-	210	211	260	94	39	13	153	0	616	-	6
Diaptomus sicilis(F)	-	119	175	87	33	0	18	799	0	98	-	26
Diaptomus sicilis(M)	-	216	236	127	31	25	3	549	0	245	-	10
Diaptomus minutus(F)	-	176	257	152	258	523	93	519	0	643	-	17
Diaptomus minutus(M)	-	121	161	43	160	445	64	547	0	319	-	20
Diaptomus oregonensis(F)	-	27	74	84	26	238	18	179	0	41	-	21
Diaptomus oregonensis(M)	-	28	36	6	10	145	48	111	0	0	-	13
Limnocalanus macrurus(AD)	-	5	8	60	125	35	34	31	0	0	-	17
Limnocalanus macrurus(IM)	-	40	21	60	25	7	18	3	0	98	-	0
Eurytemora affinis(AD)	-	0	0	0	3	0	0	0	0	0	-	0
Eurytemora affinis(IM)	-	0	0	0	3	0	6	0	0	0	-	0
Epischura lacustris(AD)	-	0	0	0	9	28	35	26	0	0	-	43
Epischura lacustris(IM)	-	0	3	0	26	17	10	3	0	0	-	25
#Station	-	6	5	3	5	3	3	4	0	2	-	3

TABLE 31. LAKEWIDE ABUNDANCE OF ZOOPLANKTON POPULATION DENSITIES ($\# \ m^{-3}$) FOR THE WATER COLUMN TWENTY METERS TO SURFACE

Species	28-03 Apr	14-17 May	04-08 June	16-21 June	17-22 July	26-31 Aug	08-12 Oct	10-14 Nov	02-13 Apr	28-31 May	6-10 Aug	17-23 Oct
Cladocera												
Leptodora	0	0	0	1	2	38	26	9	0	0	47	1
Eubosmina coregoni	23	107	646	7675	6783	1060	2254	1120	4	15	2974	2362
Bosmina longirostris	16	13	577	17117	26102	819	962	466	0	166	2324	742
Daphnia retrocurva	6	0	10	100	796	899	686	18	0	0	1430	392
Daphnia galeata	1	3	6	12	390	1388	2597	1367	28	45	1502	962
Daphnia longiremis	0	0	0	4	0	5	0	0	0	0	16	0
Ceriodaphnia lacustris	1	0	0	0	24	1	1	0	0	0	54	3
Chydorus sphaericus	0	6	66	2350	802	72	379	384	0	0	317	321
Holopedium gibberum	0	0	2	8	192	1907	1340	127	0	0	2928	404
Diaphanosoma leuch.	0	0	0	0	2	5	1	0	0	0	0	0
Polyphemus pediculus	0	0	0	0	28	38	0	0	0	0	52	0
Alona spp.	0	0	0	0	0	0	2	0	0	0	0	1
Cyclopoida												
Copepodites	530	900	2800	6720	16017	5118	10971	10456	682	1994	7071	10032
Cyclops bicuspidatus(F)	553	850	905	2909	1274	279	438	287	227	1072	458	118
Cyclops bicuspidatus(M)	665	442	580	1162	690	137	232	215	173	62	306	117
Cyclops vernalis(AD)	9	0	4	81	41	5	49	38	2	0	28	11
Cyclops vernalis(IM)	0	0	8	186	212	25	172	220	0	0	142	172
Tropocyclops	66	18	11	29	34	491	958	436	0	15	248	762
Tropocyclops	0	0	0	0	1	355	136	5	0	0	149	0
Mesocyclops edax(AD)	0	0	4	13	23	115	32	3	0	0	81	7
Mesocyclops edax(IM)	0	0	11	29	13	143	279	59	0	0	148	137
Copepod Nauplii	6696	15626	27513	53629	20170	14695	10188	8811	17283	46393	17955	3689
Calanoida												
Copepodites	101	649	3976	10374	19894	15728	14740	7962	103	3980	11288	4447
Diaptomus ashlandi(F)	279	353	289	820	257	72	31	109	755	1321	133	14
Diaptomus ashlandi(M)	192	789	265	505	201	57	15	218	652	1480	127	29
Diaptomus sicilis(F)	469	157	128	231	22	2	23	792	481	559	5	21
Diaptomus sicilis(M)	287	304	162	367	28	3	1	792	428	680	0	7
Diaptomus minutus(F)	305	256	234	389	726	859	131	995	642	1133	723	72
Diaptomus minutus(M)	272	300	169	302	566	840	93	707	477	687	676	40
Diaptomus oregonensis(F)	27	49	50	130	69	303	72	313	67	181	180	29
Diaptomus oregonensis(M)	14	35	29	80	70	228	35	229	11	8	67	29
Limnocalanus macrurus(AD)	20	16	19	51	5	17	1	18	28	0	0	0
Limnocalanus macrurus(IM)	40	75	32	37	9	24	18	0	0	0	1	0
Eurytemora affinis(AD)	0	0	0	9	10	2	2	7	0	144	3	0
Eurytemora affinis(IM)	0	0	1	13	91	1	0	8	0	0	32	0
Epischura lacustris(AD)	0	0	0	2	16	45	67	52	0	0	35	85
Epischura lacustris(IM)	0	0	0	6	107	160	194	5	0	15	58	14
#Station	19	16	26	24	23	22	19	21	14	4	12	13

TABLE 32. LAKEWIDE ABUNDANCE OF ZOOPLANKTON POPULATION DENSITIES ($\# \ m^{-3}$) FOR THE WATER COLUMN FORTY METERS TO SURFACE

Species	28-03 Apr	14-17 May	04-08 June	16-21 June	17-22 July	26-31 Aug	08-12 Oct	10-14 Nov	02-13 Apr	28-31 May	6-10 Aug	17-23 Oct
Cladocera												
Leptodora	0	0	1	6	14	34	11	2	0	0	5	7
Eubosmina coregoni	46	777	4239	34071	1074	2899	3719	1772	4	20409	1262	5373
Bosmina longirostris	19	201	4801	63576	33863	3493	2411	322	5	7502	1320	1559
Daphnia retrocurva	1	22	37	564	1809	4012	1432	0	0	547	794	532
Daphnia galeata	2	19	12	69	131	432	1016	670	68	38	530	988
Daphnia longiremis	1	0	0	0	0	0	0	0	0	0	2	0
Ceriodaphnia lacustris	0	5	0	0	0	92	10	0	0	0	0	5
Chydorus sphaericus	0	342	787	7319	53	1172	2345	579	0	660	38	1131
Holopedium gibberum	1	1	7	26	1829	1407	235	68	0	47	3162	490
Diaphanosoma leuch.	0	0	0	0	356	3	0	0	0	0	0	0
Polyphemus pediculus	0	0	0	0	0	148	0	0	0	0	155	0
Alona spp.	0	0	0	0	0	0	0	9	0	0	0	0
Cyclopoida												
Copepodites	380	1698	8288	17069	6312	4787	7848	4920	845	15315	2056	8889
Cyclops bicuspidatus(F)	412	951	560	2136	287	256	62	95	319	2042	85	96
Cyclops bicuspidatus(M)	148	476	383	1472	145	31	145	118	222	888	61	105
Cyclops vernalis(AD)	2	35	11	35	27	15	38	35	3	0	13	23
Cyclops vernalis(IM)	1	5	11	13	299	226	307	105	3	198	39	160
Tropocyclops	13	32	10	201	115	1270	1326	245	6	0	228	647
Tropocyclops	1	3	0	19	35	482	32	0	0	0	39	12
Mesocyclops edax(AD)	0	2	6	11	15	26	27	0	2	0	18	9
Mesocyclops edax(IM)	0	4	11	68	6	109	136	802	0	11	20	162
Copepod Nauplii	8879	17335	37325	43874	15613	17453	18856	2652	12133	59013	11453	4400
Calanoida												
Copepodites	345	1295	5571	12791	9907	10265	5187	2192	160	14383	4601	3756
Diaptomus ashlandi(F)	254	327	179	805	82	3	4	22	686	1154	0	26
Diaptomus ashlandi(M)	185	337	206	446	45	12	10	74	539	1985	5	34
Diaptomus sicilis(F)	266	264	85	235	5	0	0	336	371	590	0	32
Diaptomus sicilis(M)	291	367	106	457	1	0	0	276	336	724	2	2
Diaptomus minutus(F)	244	298	218	775	794	710	38	579	504	1149	2017	58
Diaptomus minutus(M)	306	350	188	475	788	409	19	253	393	1539	789	38
Diaptomus oregonensis(F)	24	55	42	246	139	65	0	164	59	143	37	43
Diaptomus oregonensis(M)	22	50	49	146	13	36	38	88	16	89	18	25
Limnocalanus macrurus(AD)	24	28	12	19	1	3	10	4	23	0	1	0
Limnocalanus macrurus(IM)	26	90	39	31	0	7	0	0	2	57	2	0
Eurytemora affinis(AD)	0	0	0	8	45	0	18	5	0	0	0	7
Eurytemora affinis(IM)	0	3	31	0	202	14	0	30	0	0	11	10
Epischura lacustris(AD)	0	0	0	6	24	76	29	20	0	0	30	92
Epischura lacustris(IM)	0	1	2	5	117	444	34	0	0	123	36	37
#Station	28	32	40	36	39	8	16	5	9	4	9	11

APPENDIX B

Water Quality Sections, Mean Zooplankton Density

Numerical densities of zooplankton are necessary for many purposes, including modeling of aquatic ecosystems. We have included this summary of densities for Southern Lake Huron for the convenience of those who need such data, although not in the detail available in the complete data set and not corrected for net efficiency.

TABLE 33. SEASONAL WATER QUALITY SECTION SUMMARY FOR THE WATER COLUMN LESS THAN TEN METERS

		Sections						
	Season	4	5	6	7	8	9	10
Eubosmina coregoni	Spring	181.3±213.2* 0-478(14)**	3948.1±8123.1 0-37368(24)	360.9±639.0 0-8302(28)	66.7±80.6 0-216(7)	9.2±14.9 0-56(15)	103.4±273.6 0-920(11)	0 0
	Summer	4788.6±6676.1 12-25498(16)	20167.6±28712.7 169-111010(30)	11891.4±35177.7 188-198853(33)	3222.8±4043.5 86-10799(9)	1272.5±1560.2 0-5452(14)	3189.6±3911.8 52-16044(16)	835.1±790.2 9-2322(6)
	Fall	2632.7±3298.0 45-8696(11)	9614.5±12985.8 135-43855(20)	3332.5±4499.0 60-15821(22)	714.4±739.5 45-1630(6)	833.5±676.5 317-1902(8)	862.8±651.4 301-1887(10)	No data
Bosmina longirostris	Spring	315.7±748.6 0-2807(14)	964.8±9104.5 0-32699(24)	354.0±942.6 0-4856(28)	43.5±46.8 11-138(7)	27.7±46.4 0-173(15)	98.7±210.0 0-678(11)	3.1±5.3 0-9(3)
	Summer	18974.5±26563.2 165-88054(16)	45921.8±76225.5 241-295927(30)	27911.1±55589.0 64-247601(23)	4450.0±5404.8 188-13996(9)	3624.2±3826.9 45-9298(14)	7033.0±11012.7 211-26515(16)	1307.9±867.6 0-2581(6)
	Fall	512.0±253.7 0-2581(11)	2111.5±2731.1 158-5283(20)	1041.9±1082.9 90-3562(22)	298.1±335.4 90-951(6)	234.7±(118.6) 90-452(8)	588.7±483.5 150-1358(10)	No data
Eurytemora affinis	Spring	3.8±13.8 0-50(13)	17.1±38.1 0-158(24)	3.2±14.4 0-75(28)	0 0	0 0	0 0	3.7±6.4 0-11(3)
	Summer	45.1±81.6 0-226(16)	102.4±239.7 0-188(30)	32.6±106.1 0-314(32)	10.3±13.4 0-30(9)	10.8±28.1 0-90(14)	19.8±41.8 0-163(16)	159.9±319.8 0-799(6)
	Fall	7.8±18.5 0-56(11)	139.8±245.9 0-981(20)	32.1±113.5 0-529(22)	0 0	13.1±37.1 0-105(8)	10.5±22.4 0-60(10)	No data
Nauplii	Spring	12467.3±6066.4 2931-23968(14)	14672.2±24687.9 993-120702(22)	10782.3±9436.7 107-46847(27)	18901.6±12230.8 9245-38619(7)	8992.9±6761.2 3208-28563(15)	10832.6±9339.2 2288-27677	21289.5±8287.7 1153-26753(3)
	Summer	1584.6±15319.8 4253-64932(16)	10933.0±9955.4 2224-49728	14808.6±10284.2 1870-43130(32)	11040.9±6146.1 4311-19547(9)	16337.2±13130.4 2862-55928(14)	13490.8±7605.3 4551-29521(15)	24634.2±17749.0 12907-59072(6)
	Fall	9114.6±4421.6 4560-18672(11)	13572.6±6846.5 460-30707(20)	11417.1±6487.2 2657-22237(22)	12246.3±7350.4 6026-25000(6)	8891.1±3562.7 5338-15716(8)	9240.5±1920.4 6340-12228(10)	No data

*MEAN±1 ST. DEV.
**RANGE(N)

		Sections						
	Season	4	5	6	7	8	9	10
Cladocerans (AD+COPS)	Spring	514.7±884.1* 15-3386(14)**	8821.9±18257.9 0-77835(24)	751.8±1532.0 0-7458(28)	120.5±105.0 15-320(7)	45.8±56.8 0-181(15)	206.8±477.0 4-1598(11)	8.1±9.5 0-18(3)
	Summer	27606.4±28646.2 1621-97511(16)	72574.8±11065.8 2716-468250(30)	43045.3±95026.0 1168-186003(32)	9117.2±10085.0 211-22601(9)	5703.2±5795.3 452-14853(14)	9876.1±10141.1 264-36266(16)	3044.4±1989.5 0-3906(6)
	Fall	5562.1±4856.1 888-12869(11)	17200.5±20765.1 505-78804(20)	10984.8±15005.3 61-65019(22)	5036.0±2855.9 1087-9699(6)	5002.0±1805.5 2628-7714(8)	5274.1±4160.8 1057-14251(10)	No data
Cyclopoids (AD+COPS)	Spring	2337.1±2408.2 298-8099(14)	5030.6±6552.5 196-23823(24)	1589.5±1441.5 61-5505(28)	1750.1±749.6 1094-2846(7)	2610.1±3923.7 54-12850(15)	1679.1±1211.8 354-4381(11)	1011.3±383.5 622-1389(3)
	Summer	7068.4±6317.9 588-19358(16)	8637.2±9612.6 582-38914(30)	5479.6±5344.4 116-23906(32)	5794.9±5170.8 1206-15624(9)	7912.2±6800.4 1231-23906(14)	7853.7±5439.6 1108-11990(16)	3632.2±2037.4 1460-5648(6)
	Fall	10952.3±4511.0 4220-17210(11)	12911.9±6202.0 505-23626(20)	11461.3±4532.2 2234-20078(22)	14059.6±6780.5 1428-23457(6)	9638.5±5577.5 1695-16350(8)	14225.3±4959.6 8092-24381(10	No data
Calanoids (AD+COPS)	Spring	2710.9±2739.8 253-10894(14)	2481.6±1194.3 927-21478(24)	1970.4±1459.7 150-5109(28)	2082.8±616.5 1291-2969(7)	2324.2±2438.1 588-9878(15)	1854.8±914.0 404-3182(11)	4471.3±4101.7 1787-9193(3)
	Summer	8671.3±6963.5 1852-15851(16)	4791.7±3935.4 555-41553(30)	11078.8±6706.3 2261-82853(32)	7831.5±6311.5 2081-21663(9)	5804.2±7354.8 45-14853(14)	12425.4±6469.1 3913-23550(16)	11905.7±4429.3 4506-16552(6)
	Fall	7065.0±4636.3 1444-15126(11)	5577.9±3725.8 641-15579(20)	12842.3±8577.2 1162-41666(22)	16153.7±6313.6 8605-24192(6)	20505.2±10591.8 12062-44068(8)	16298.1±10143.0 3252-36081(10)	No data

*MEAN±1 ST. DEV.
**RANGE(N)

TABLE 34. MONTHLY WATER QUALITY SECTION SUMMARY FOR THE WATER COLUMN LESS THAN TEN METERS

	Eubosmina coregoni	Bosmina longirostris	Eurytemora affinis	Calanoida	Cyclopoida	Cladocera
AREA 4						
April 28-03 n=5	28.9±14.2	15.1±4.7	0±0	1023.6±228.6	684.8±141.0	49.1±14.1
May 14-17 n=3	94.5±27.4	16.7±4.3	0±0	1692.0±309.8	1278.1±97.2	116.2±25.7
June 04-08 n=6	351.7±94.7	715.9±432.2	12.5±8.5	4626.3±1373.6	4346.7±970.9	1101.8±466.4
June 16-21 n=5	6202.1±2245.0	16918±8467.5	1.5±1.5	13513.4±4302.6	7968.5±2911.7	24442.6±10284.3
July 17-22 n=5	2959.3±965.8	71724.1±15393.2	89.3±39.8	3988.3±683.6	2848.0±1538.4	46813.1±16370.7
August 26-31 n=6	5015.1±4133.1	1729.9±771.0	69.1±41.0	8537.0±2005.1	8339.0±3273.5	11553.9±8052.5
October 08-12 n=5	4840.3±1703.7	962.5±506.4	17.3±11.4	9654.9±2517.2	7435.3±1564.9	9331.6±1951.7
November10-14 n=6	843.1±498.2	136.6±55.9	0±0	4906.9±944.0	13883.1±1170.8	2437.6±1024.5
AREA 5						
April 28-03 n=6	33.9±7.3	84.8±51.4	0±0	891.3±325.2	423.2±86.8	62.8±20.1
May 14-21 n=8	1469.8±1303.0	34.9±123.3	5.7±5.6	2661.5±303.0	3169.4±1120.5	2565.2±2310.1
June 04-08 n=10	8279.9±3486.2	9215.5±3983.6	100.5±69.0	2875.8±341.4	9284.2±2417.6	19076.9±7848.7
June 16-21 n=10	39799.4±12796.6	83171.5±34634.2	16.8±7.4	6160.3±1777.5	16357.1±3810.1	138948.8±51934.7
July 17-22 n=10	1052.9±1860.1	51385.5±17452.5	229.7±122.0	2189.4±275.0	3463.1±581.6	64211.4±18913.1
August 26-31 n=10	4204.7±2019.7	1208.7±408.5	27.2±14.8	4921.4±781.8	5091.3±2081.0	13272.5±4512.9
October 08-12 n=10	13096.9±5349.1	3041.7±1144.2	207.2±96.1	4960.2±1019.7	9834.1±1722.8	23282.1±7740.1
November10-14 n=10	6132.1±2071.5	1281.6±239.8	93.4±51.1	6195.7±1343.8	15989.7±1745.5	11119.1±2704.4

	Eubosmina coregoni	Bosmina longirostris	Eurytemora affinis	Calanoida	Cyclopoida	Cladocera
AREA 4						
April 28-03 n=5	28.9±14.2	15.1±4.7	0±0	1023.6±228.6	684.8±141.0	49.1±14.1
May 14-17 n=3	94.5±27.4	16.7±4.3	0±0	1692.0±309.8	1278.1±97.2	116.2±25.7
June 04-08 n=6	351.7±94.7	715.9±432.2	12.5±8.5	4626.3±1373.6	4346.7±970.9	1101.8±466.4
June 16-21 n=5	6202.1±2245.0	16918±8467.5	1.5±1.5	13513.4±4302.6	7968.5±2911.7	24442.6±10284.3
July 17-22 n=5	2959.3±965.8	71724.1±15393.2	89.3±39.8	3988.3±683.6	2848.0±1538.4	46813.1±16370.7
August 26-31 n=6	5015.1±4133.1	1729.9±771.0	69.1±41.0	8537.0±2005.1	8339.0±3273.5	11553.9±8052.5
October 08-12 n=5	4840.3±1703.7	962.5±506.4	17.3±11.4	9654.9±2517.2	7435.3±1564.9	9331.6±1951.7
November 10-14 n=6	843.1±498.2	136.6±55.9	0±0	4906.9±944.0	13883.1±1170.8	2437.6±1024.5
AREA 5						
April 28-03 n=6	33.9±7.3	84.8±51.4	0±0	891.3±325.2	423.2±86.8	62.8±20.1
May 14-21 n=8	1469.8±1303.0	34.9±123.3	5.7±5.6	2661.5±303.0	3169.4±1120.5	2565.2±2310.1
June 04-08 n=10	8279.9±3486.2	9215.5±3983.6	100.5±69.0	2875.8±341.4	9284.2±2417.6	19076.9±7848.7
June 16-21 n=10	39799.4±12796.6	83171.5±34634.2	16.8±7.4	6160.3±1777.5	16357.1±3810.1	138948.8±51934.7
July 17-22 n=10	1052.9±1860.1	51385.5±17452.5	229.7±122.0	2189.4±275.0	3463.1±581.6	64211.4±18913.1
August 26-31 n=10	4204.7±2019.7	1208.7±408.5	27.2±14.8	4921.4±781.8	5091.3±2081.0	13272.5±4512.9
October 08-12 n=10	13096.9±5349.1	3041.7±1144.2	207.2±96.1	4960.2±1019.7	9834.1±1722.8	23282.1±7740.1
November 10-14 n=10	6132.1±2071.5	1281.6±239.8	93.4±51.1	6195.7±1343.8	15989.7±1745.5	11119.1±2704.4

Table 34 (continued)

	Eubosmina coregoni	Bosmina longirostris	Eurytemora affinis	Calanoida	Cyclopoida	Cladocera
AREA 6						
April 28-03 n=8	19.5±17.8	3.2±1.5	0±0	869.8±155.2	385.1±139.5	25.2±18.4
May 14-17 n=9	201.8±130.1	70.5±36.9	0±0	2025.7±426.1	1903.5±557.2	349.4±182.6
June 04-08 n=11	709.8±298.3	840.7±494.9	8.2±8.0	2643.8±636.6	2284.9±441.1	1609.8±770.0
June 16-21 n=11	33531.8±17299.5	61340.8±25317.1	8.9±4.5	8803.2±1799.1	10461.0±1768.6	97975.2±44585.1
July 17-22 n=10	4631.2±1625.1	21900.4±8211.9	86.3±57.8	7289.9±1150.4	2587.9±1027.9	23249.6±10023.8
August 26-31 n=11	841.6±127.3	492.2±88.2	4.9±3.7	16863.6±1785.7	3128.1±560.1	6111.3±985.6
October 08-12 n=11	4851.2±1592.5	173.1±349.1	50.1±47.9	13913.1±3483.8	12310.4±1617.1	18200.1±5521.4
November 10-14 n=11	1795.5±954.4	325.2±87.0	13.6±9.9	11771.1±1295.3	10511.8±1056.7	3842.1±1427.5
AREA 7						
April 28-03 n=1	0	15.1	0	1291.2	1094.4	15.1
May 14-21 n=3	25.7±5.5	22.6±11.3	0±0	1864.0±63.4	1446.6±168.5	59.6±10.8
June 04-08 n=3	96.6±63.5	73.9±35.3	0±0	2565.5±362.3	2272.0±528.7	183.3±69.9
June 16-21 n=3	250.7±82.5	177.9±37.0	0±0	3085.9±673.8	5570.5±1962.2	428.6±109.9
July 17-22 n=3	8378.6±1213.0	11189.0±1611.0	27.5±2.4	5995.1±1090.6	4647.8±3377.6	22134.3±281.4
August 26-31 n=3	1039.2±479.3	2049.9±1163.2	0±0	14413.7±4106.1	7166.1±4332.0	4788.6±2764.8
October 08-12 n=3	1278.1±367.4	460.4±255.5	0±0	16062.0±4512.1	17340.3±4832.9	6559.6±1687.1
November 10-14 n=3	150.6±54.3	135.6 45.3	0±0	16425.3±3584.7	10779.0±2047.6	3472.3±1226.8

Table 34 (continued)

	Eubosmina coregoni	Bosmina longirostris	Eurytemora affinis	Calanoida	Cyclopoida	Cladocera
AREA 8						
April 28-03 n=4	2.8±2.8	0±0	0±0	7.4±4.4	757.5±194.1	673.3±314.0
May 14-17 n=5	7.2±3.3	6.2±3.1	0±0	22.2±2.0	831.9±217.8	1954.1±245.4
June 04-08 n=6	15.1±8.9	64.1±23.5	.2±.1	94.9±26.0	5327.1±2162.6	3616.5±1437.2
June 16-21 n=6	121.4±28.6	312.9±143.0	10.0±32.6	459.3±181.0	12605.6±3329.7	9868.8±2286.4
July 17-22 n=5	2279.5±878.7	6145.3±1342.7	30.3±19.1	9421.7±2189.7	5585.6±857.7	6104.2±1163.6
August 26-31 n=3	1937.0±506.7	5044.8±2190.9	0±0	9993.0±2898.1	2403.3±772.2	1524.4±5916.3
October 08-12 n=2	1124.7±762.3	347.2±105.6	0±0	4808.0±996.8	12454.0±3396.9	16273.5±3955.4
November 10-14 n=6	945.2±284.0	413.6±154.0	17.5±17.4	5096.6±846.9	8714.8±2399.9	21916.1±4852.0
AREA 9						
April 28-03 n=3	14.6±3.8	0±0	0±0	22.8±8.8	1091.9±201.3	956.3±277.6
May 14-21 n=3	5.3±1.0	2.5±1.2	0±0	9.1±2.2	1115.5±91.6	1398.9±345.6
June 04-08 n=5	269.6±169.5	215.7±125.6	0±0	435.9±299.4	2369.5±707.8	2607.7±210.6
June 16-21 n=5	1320.3±344.7	1536.2±423.3	0±0	2926.8±745.7	10900.0±3903.2	7938.1±1446.7
July 17-22 n=6	6027.9±2210.9	10141.2±3529.6	42.5±25.8	17600.1±5255.7	7685.3±1077.6	13395.0±1887.0
August 26-31 n=5	1652.7±380.9	1600.2±658.3	31.7±31.7	7545.8±1945.0	3669.4±958.7	15749.2±398.1
October 08-12 n=5	5970.4±3436.0	763.8±247.7	0±0	8392.3±1569.1	13144.5±3663.0	22458.8±4685.9
November 10-14 n=5	945.2±311.2	413.6±168.7	21.0±13.0	2156.0±683.4	12696.2±2222.7	9033.5±2350.2

Table 34 (continued)

AREA 10	*Eubosmina coregoni*	*Bosmina longirostris*	*Eurytemora affinis*	Cladocera	Cyclopoida	Calanoida
April 28-03 n=0	-	-	-	-	-	-
May 14-17 n=1	0	0	0	5.7	622.1	1787.5
June 04-08 n=2	0•0	4.7•4.6	5.6•5.5	9.3•9.2	1205.9•183.0	5813.6•3379.5
June 16-21 n=2	1166.1•1156.6	765.5•765.4	0•0	1958.0•1948.5	3554.6•2093.9	6661.0•1719.4
July 17-22 n=2	750.4•64.1	1969.5•612.0	399.7•399.7	2798.9•544.3	5116.8•941.3	14223.0•45.1
August 26-31 n=2	588.8•203.8	1188.9•418.9	0•0	4376.0•1669.4	2225.0•175.4	14833.0•1719.4
October 08-12 n=0	-	-	-	-	-	-
November10-14 n=0	-	-	-	-	-	-
AREA						
April 28-03 n=						
May 14-21 n=						
June 04-08 n=						
June 16-21 n=						
July 17-22 n=						
August 26-31 n=						
October 08-12 n=						
November10-14 n=						

APPENDIX C

Graph of Lakewide Zooplankton Density

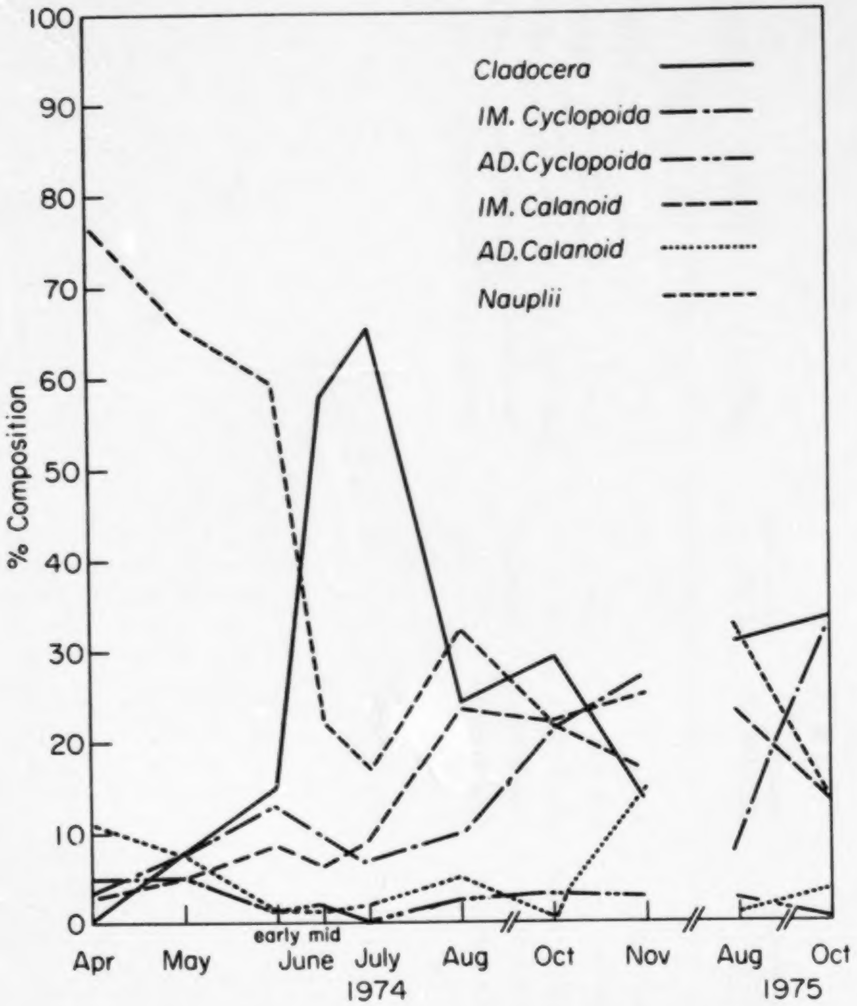

Figure 44. Percentage composition of crustacean zooplankton in Southern Lake Huron in 1974-1975 (IM:Immature, AD:Adult).